VARIATION AND SPECIATION

IN THE GRASSHOPPERS OF THE CONALCAEINI

(ORTHOPTERA: ACRIDIDAE: MELANOPLINAE):

THE LOWLAND FORMS OF WESTERN MEXICO,

THE GENUS BARYTETTIX

THEODORE J. COHN
DEPARTMENT OF ZOOLOGY
CALIFORNIA STATE UNIVERSITY, SAN DIEGO

AND

IRVING J. CANTRALL
MUSEUM OF ZOOLOGY
UNIVERSITY OF MICHIGAN

Frontispiece. Laboratory reared first generation *Barytettix* from field collected parents, all from Sinaloa, México.

Upper left.   *Barytettix poecilus* (Hebard), adult male (length of body about 24 mm), 20 mi NW Mazatlán Cathedral.

Upper right.   *Barytettix nigrofasciatus* Cohn and Cantrall , third instar nymph (length of body about 17 mm), 1.1 mi SW San Ignacio Ferry.

Middle and lower left.   *Barytettix tridens* Cohn and Cantrall , adult male (length of body about 27 mm), 16.4 mi N Los Mochis turnoff.

Middle and lower right.   *Barytettix psolus* Cohn and Cantrall , adult female (length of body about 38 mm), 14 mi NW Culiacán Cathedral.

CONTENTS

INTRODUCTION

Members of the genus *Barytettix* are among the commonest and most conspicuous grasshoppers of the northwestern coastal plain of mainland México. Between the coast and the Sierra Madre Occidental and from Arizona into the Trans-Volcanic Belt, they occur in many natural habitats as well as in most of the weedy environments created by man. Although short-winged, they are active and are strong jumpers. In view of this behavior and apparently broad habitat tolerance, one might expect extensive distributions and little speciation or geographic variation in the genus. The reverse is true. Eight species and at least seven subspecies are found between Arizona and Colima, and a ninth species occurs as an isolate in Baja California. Only three species have broad distributions. These, together with the other members of the genus, show complex patterns of overlap, contiguity, and allopatry. Almost all display some degree of geographic variation, and in several forms this variation is striking.

A genus such as *Barytettix* is ideal for the study of a number of evolutionary problems. Further, these grasshoppers are easy to observe and collect in the field, and most, if not all, of the species are easy to breed and to rear in the laboratory. Obvious problems which might be studied include the nature, development, and maintenance of geographic variants, the nature and extent of gene flow between populations and between demes of populations, competitive and reproductive exclusion, and the possibility of stasipatric speciation. Because of the variety of patterns of allopatry and sympatry among closely related species, the genus offers exceptionally good material for the study of reproductive isolation in animals which lack obvious precopulatory isolating mechanisms. *Barytettix* has provided new evidence for the role of mechanical isolation in reproduction (Cantrall and Cohn, 1972) and at present is being further studied in laboratory crosses in an attempt to learn the effectiveness of this mechanism in these grasshoppers.

Our study is incomplete in many respects, but since further refinement of the systematics and biology of these insects will require much more time and more intensive effort, we feel that we have reached the point where it is important to make known the basic taxonomic situation of this group of common but largely unknown grasshoppers. It is perhaps even more important that we now outline those biological situations found in the genus which appear to have a significant bearing on basic biological problems and which new material and new approaches might clarify.

In the near future we hope to complete our studies on the tribe Conalcaeini described herein and to publish descriptions of two new genera and a review of *Conalcaea*. These genera along with *Barytettix* comprise the tribe as we now understand it.

In 1951 Gurney published an account of the Conalcaea Complex in which he brought together widely scattered relevant information, reported on type examination and identification, and most ably summarized the existing knowledge of *Barytettix*. His revision is the foundation upon which we have based our study. Previous literature consisted largely of single descriptions, records of distribution, and similar details.

ACKNOWLEDGEMENTS

knowledge of the land, the people, and the customs of México, has materially eased the way for effective field work in a foreign country. George E. Radwin, San Diego Museum of Natural History, and Vincent Roth, American Museum of Natural History Southwestern Research Station, have aided our cause through the gift of specimens. Henry van der Schalie, The University of Michigan Museum of Zoology, generously had cross-sections of selected bursae prepared in his microtechnique laboratories. James Mathewson of the Chemistry Department, California State University, San Diego, arranged for the use of that department's lyophilizer and gave generously of his time and expertise in the freeze-drying of the 1970 collections.

Martha B. Lackey and John Tottenham have borne up remarkably under our demands for the many illustrations which they have prepared for us. Mrs. Lackey prepared all of the plates and the major portion of the illustrations. John Tottenham rendered Fig. 7 A and B, Fig. 9 A-F, and Fig. 13 A-F. The photographs for the Frontispiece were taken by Dallas Clites of San Diego. Ruth Fausett has painstakingly and with much patience arranged, typed and retyped the many revisions of the tables in the interest of accuracy and clarity and sometimes according to the whims of authors and editor. Final copy of the tables was produced on an IBM Composer typewriter at California State University, San Diego. Mary Snider and Dorothy B. Hodgman of Ann Arbor, Michigan, struggled with our much amended, interlined, corrected, and often scribbled early drafts and successfully transcribed them to produce readable copy. Gwen Gardner of the Word Processing Center, California State University, San Diego, did the final typing of the manuscript.

The 1970-71 rearing project in Tucson was conducted in quarters supplied by the Cotton Insects Biological Control Investigations of the United States Department of Agriculture. D. I. Bryan, R. E. Fye, and G. D. Butler of that organization, and W. E. Nutting of the University of Arizona generously helped with many practical problems. Richard V. Carr, then at the University of Arizona, helped set up the project and assumed responsibility for it during the long periods when Cohn was in México or Michigan. It was largely through his efforts, later continued by Steven Moore and Richard Sackett, that this phase was so successful. In Culiacán, the grass-

hoppers were reared with care and affection by Srta. Pauline Stopol aided by Dora Stopol, in quarters generously and with much tolerance supplied by Simon and Guadalupe Stopol. Throughout the 1970-71 season, Jean W. Cohn aided in all phases of the work, constructed all the cages and solved many practical problems when all else failed. Her moral support kept the work going at high pitch, and her companionship and physical support enabled the field and rearing work to advance under the most difficult circumstances.

Financial support from the Sigma Xi Research Fund and from the American Philosophical Society facilitated Cohn's study of *Neobarrettia* in 1958 and 1959 during which he also collected *Barytettix*, and funds from National Science Foundation Grant No. G 14012 to T. H. Hubbell, Emeritus Director of The University of Michigan Museum of Zoology, enabled us in 1961 to collect along a transect of the Sierra Madre Occidental as well as at various localities in Sinaloa, Nayarit and central Jalisco.

To each of these individuals, and to those responsible for the granting of financial aid, we wish to extend our thanks, and to indicate grateful appreciation for the many gestures which, in large part, made this study possible.

MATERIALS

Our initial interest in the genus *Barytettix* was stimulated by the incidental collection of members of the distinctive Psolus Group. These were taken by Cohn during the fall periods of 1958 and 1959 while he was doing field work on the tettigoniid genus *Neobarrettia*. Since that time, and as our studies of *Barytettix* developed, additional field work has seemed desirable in order to work out some of the many details of distribution and phyletic relationships which became apparent. Cohn, once accompanied by Cantrall, returned specifically to study *Barytettix* for periods of from one to four weeks in five separate years. Most work was done along the main west coast Mexican Highway No. 15 during the summers when rains make dirt side roads almost impassable. A transect was made along the Durango-Mazatlán Highway, and collections have been made in the foothills farther north near Cosalá and Alamos. Terrain along roads leading towards the base of the Sierra Madre Occidental near San Ignacio, Tepuche, and Tezopaco has

been investigated, and, in the summer of 1970 and at the behest of Cohn, James Melli and John Stallone worked along roads leading to the base of the mountains near Badiraguato, as well as east of Sanalona, and well into the mountains on a road running east from Alamos.

A desire to further clarify population inter-relationships resulted in Cohn returning to México during the summer and fall of 1970, during which time he carried out an extensive program of collecting along Highway No. 15. Much living material was returned to Culiacán, or to Tucson, Arizona, where, with the exception of *crassus*, nymphs of all known taxa of *Barytettix* were reared to maturity, and many infra- and interspecific crosses were attempted. The clarification of certain aspects of mechanical reproductive isolation in *Barytettix* made observations on the mating behavior of caged individuals desirable, and, as a result, a number of pairs *in copula*, both intra- and interspecific, were frozen and then preserved in alcohol. Although some of the results of Cohn's 1970 activities are included in this paper, results from crosses, observations, and study of dissections of copulating pairs will be reported at a later date.

The bulk of the large collection of *Barytettix* amassed by the above efforts is deposited in The University of Michigan Museum of Zoology Collections. Specimens discussed or listed in the present study without an indication of ownership are a part of this material. Representative specimens from this assemblage, when available, will be deposited in the major world Orthopterological Centers, and in the collections of the Instituto de Biología de la Universidad Nacional de México, designated by the authorities of the Mexican Government as a depository for samples of specimens collected under permit (*in litt.*, Dr. Carlos Márquez Mayaudón, 1971).

During the course of our studies, it has been necessary to examine a number of specimens from the holdings of both the Academy of Natural Sciences of Philadelphia (ANSP), and of the United States National Museum (USNM).

METHODS

MALE GENITALIA.— A comprehensive analysis of the components of *Barytettix* would not have been possible without a thorough study of the male concealed genitalia and of the female complementary structures. Museum specimens must

be softened before these organs can be moved or dissected without destruction. Depending upon the time element several methods have been employed. A few minutes in hot water, a little longer in ammonia, perhaps twenty minutes submerged in cold water, or sandwiched overnight between several layers of water-saturated paper hand toweling creates the desired amount of relaxation.

After relaxation of a male, the specimen is positioned[1], and, using insect pins with the tip bent at a right angle, the pallium is slipped back and the subgenital plate lowered with one rotating motion. One bent insect pin is inserted into the genital cavity anterior to the genital mass in such a way that the tip of the pin is pointing ventrally; a second bent pin is inserted behind the mass and with the tip also pointing ventrally. The tips of the pins are rotated upward and toward each other simultaneously. These movements roll the genitalia upward and out of the genital cavity, and into position for examination. Since most studies can be made from such preparations the extruded genital mass was usually left in place to dry. Occasionally it is desirable to make a more thorough and detailed examination. In such cases, the membranes and muscles holding the genital mass in place are cut and the mass transferred to a macerating agent.

We have found the acid corrosive solution[2] suggested by Mitchell and Cook (1952) most useful for maceration. This fluid offers several advantages in that the genital structures are not discolored or distorted, heat is not necessary, staining can be accomplished with ease, and the genital mass can be left in the fluid for any length of time without loss of fine structure. Disadvantages are that the fluid does not seem to work well on newly killed animals, nor on those preserved in alcohol or formalin. By far the best results are obtained with material which has been dried and then relaxed. Tissue destruction requires five or more hours, preferably overnight. Now and then, it is desirable or necessary to place new solution on a specimen before the

---

[1]For this purpose a sheet of pinning surface large enough to cover the microscope stage is used. To this is glued a cork stopper. The stopper should be wide enough to support the grasshopper abdomen when the grasshopper is pinned in place over the stopper. Lateral movement of the abdomen is prevented by bracing with a pair of insect pins.

[2]Formula: 9 gm chloral hydrate, 6 cc glacial acetic acid, 9 cc distilled water. The fluid can be prepared in quantity and keeps indefinitely. It is best not to reuse the solution.

desired results are obtained. The process can be accelerated by stirring the solution from time to time. As is the case with potassium hydroxide, the membranous and sclerotized genital parts must be brushed free of the softened tissue after maceration. Membranes and feebly sclerotized parts are quite transparent and are better seen if the cleared genital mass is transferred to acid fuchsin and stained for from five to ten seconds, or up to a minute, depending on the size and thickness of the mass and its membranes. The mass is then washed with 70% ethanol, drained, and stored in glycerin.

FEMALE GENITALIA.– A preparation of the female copulatory structures can be made by first cutting the inter-segmental membrane between the 8th and 9th abdominal segments of a relaxed female. The tip of the abdomen is then pulled caudally until the viscera can be cut anterior to the spermatheca. The tergal sclerites and the supra-anal plate are removed from the part of the body which has been dissected away, and are oriented and reattached to the top of the female's body by means of clear lacquer. The remainder of the dissection is placed in acid corrosive overnight. The dorsal ovipositor valves are then removed, and a cut along the anterior margin of the basivalvular sclerites is made to separate the subgenital plate and ventral portions of the genital cavity from the ventral ovipositor valves and the dorsum of the genital cavity and attached receptaculum seminis. The structures are stained in acid fuchsin. All parts permanently removed from the pinned specimen are stored in glycerine.

FIELD PROCEDURES.– One of the more perplexing problems of the orthopterist is the evaluation of the significance of coloration as a taxonomic tool. This is not helped by preservation which, more often than not, is so poor that difficulty in color interpretation is experienced. We have for many years attempted to improve on this situation by experimenting with a number of techniques which might yield better study material. The most practical method has turned out to be the layering of freshly killed specimens (often gutted) between sheets of cellucotton in a cigar box, or by arranging the specimens on a sheet of cotton which in turn is wrapped in paper to produce a small flat packet. The packets are placed in cigar boxes or other suitable containers. The containers, whether holding packets or layered specimens, are tied under the hood of an automobile and exposed to heat of the engine as the vehicle is operated. Circulation of warm air is essential to this method and to that end the tops and bottoms of the containers have been fitted with screen covers.

In 1970 Cohn vastly improved on the layering technique by placing freshly collected specimens in a portable "Norcold" freezer operated by power from the car battery. Such material eventually reached the laboratory where it was thawed, layered in cellucotton as described above, refrozen, and then transferred to a large lyophilizer operating at room temperature and with a vacuum of a few tenths of a millimeter of mercury. Complete dessication of five cigar boxes at a time, each containing from 100 to 200 specimens, was accomplished in from three to four days. Color preservation appears to have been excellent, although there may have been some slight fading of the greens. The only problem we have encountered to date with this method is a slight difficulty in lifting up or moving the male concealed genitalia. This appears to result from the excellent preservation of the muscles which are rather elastic when relaxed and thus tend to draw the genitalia back into the abdominal cavity. Application of household ammonia to the parts facilitates the dissection.

COLORATION.– Individuals of the genus *Barytettix,* as they rest in the vegetation, are striking insects. The colors are bright and the blotches and stripes of the color patterns are sharply defined. Red, orange, brown, yellow, gray, olive-green, green, blue, and purple appear as distinctive colors. However, upon examination of series of specimens we have found that there is considerable variation in the tone of a given color, both within a population and between populations. Tibial color may be polymorphic in a given deme, and we have reason to believe that large samples might well show continuous variation from one extreme to another. For these reasons we have deliberately avoided attempting to indicate hue or shade. Our terminology may thus seem rather broad and arbitrary, but there is functionally little or no difficulty in recognizing the color indicated. We have used the term bicolored with reference to hind tibial color when the proximal and distal ends of the tibia are of distinguishably different colors. In all such cases, the transition between

the two colors is gradual; in no case did we find them sharply separated.

KEYS AND TABLES.— Although dichotomous keys are probably necessary for the separation of large numbers of taxa, and, in abbreviated form, may have definite value in facilitating rapid identification, they often have serious limitations. From a strictly practical viewpoint, they may be unreliable. An error in interpretation of a single rubic, or the absence of a major character in a couplet, or poor preservation of a single key character in a given specimen may prevent identification. An undescribed species cannot be classified with assurance, and may require a major revision of the key in order to include it. Most of these deficiencies are eliminated in a table. As pointed out by Newell (1970), a table includes each character for each taxon, and thus can show similarities as well as differences. A detailed and well-constructed table can be open-ended, permitting the insertion of new species with little or no change. Finally, and most important, a table lends itself to computerization and, if complete, greatly facilitates data storage and retrieval. For these reasons we have presented our keys in tabular form.

MEASUREMENTS.— All measurements are presented as ranges, or in bar histograms. Since many of the specimens we have examined were not collected randomly, and since all species of *Barytettix* are readily recognizable on the basis of morphological features, we feel that a detailed statistical analysis of mensural characters would be inappropriate at the present time.

Measurements were taken in the following ways:

Body Length.— From the anterior margin of the fastigium of the vertex to the distal edge of the genicular lobe of the caudal femur with the femur aligned parallel to the axis of the body.

Length of Pronotum.— Taken along the median carina.

Length of Metazona.— Taken along the median carina.

Length of Caudal Femur.— From the anterior edge of the upper basal lobe to the distal edge of the genicular lobe.

Length of Cephalic Femur.— The length of a line along the posterior surface of the appendage from the distal edge of the genicular lobe to the dorsal junction with the trochanter.

Length of Male Supra-Anal Plate.— Maximum possible length.

Length of Tegmina.— Length of a line running from the tip to the junction of the ventral (costal) margin of the tegmina with the caudal margin of the pronotum. Owing to the positioning of the pronotum as a result of pinning, a certain amount of inaccuracy exists in this measurement.

Width of Caudal Femur.— Maximum possible measurement.

Width of Tegmina.— Maximum possible measurement.

Width of Male Supra-Anal Plate.— Maximum possible measurement.

Aedeagal Measurements.— These are indicated and discussed under the section dealing with the terminology of the male genitalia (page 14).

DRAWINGS.— All stippled illustrations of aedeagal structures have been drawn from cleared material, or from phallic masses which have been moistened with household ammonia until all membranes have swollen to the condition found in fresh specimens.

THE MALE CONCEALED COPULATORY STRUCTURES

During the past three decades much progress has been made in the evaluation of the taxonomic and biological significance of the concealed genitalia of male Acridoidea. A steady increase in the use of the diversity in these structures as differentiating characters has resulted in the publication of several efforts to clarify terminology in the hope that a better understanding of homology and relationships might be obtained.

The approach was begun by Roberts (1941) and was improved upon and greatly expanded by Dirsh (1956). Both of these projects have been reevaluated recently by Kevan, Akbar, and Chang (1969) who not only ably summarized the work of Roberts and Dirsh, but attempted a further refinement by blending in the results of an extensive literature survey.

The concealed genitalia of male *Barytettix*

can be categorized into three groups based on the size and shape of the aedeagal parts. Figure 1 shows the relationships of these aedeagal elements, one to another within a given group, and indicates homologies between the groups. Although our nomenclature largely follows that set forth by Kevan, et al (1969), we have deviated to some extent in the interests of simplicity and clarity, or to indicate relationships more or less peculiar to *Barytettix*. Further, in the course of this study, we have had occasion to measure certain of the aedeagal elements. A number of terms, aedeagal measurements, and intrageneric relationships of these parts are presented and discussed or defined below.

The epiphallus shows little interspecific variation in *Barytettix*. In structure it is typically melanoploid in that a well-defined and undivided bridge is present, as are lophi and ancorae. Oval sclerites are lacking.

The dorsal aedeagal valves and sclerites become variously involved with the sheath (SH in Fig. 1 A and B) to such an extent that it is often difficult to recognize the point of contact between the elements. In the interests of simplicity we are referring to these fused structures as the dorsal valves (DV in Fig. 1). In *Barytettix* the dorsal valves are fused proximally. The distal tips, herein referred to as the *free lobes of the dorsal valves*, may each have an essentially straight medial margin, or the margin may be curved, feebly sinuous, notched, or the notch may be deep enough to produce an aciculate process (see Figs. 10; 14 A-F).

The sheath is well-developed in this genus of grasshoppers. Not only does it contribute much to the size and shape of the dorsal valves, but it extends around the lateral and ventral portions of the base of the aedeagus. There it forms a collar (SH in Fig. 1 A and B) or it may be enlarged and elongated to produce a flattened (VLSH in Fig. 1 E and F) or a finger-like protrusion (VLSH in Fig. 1 C and D). We are referring to the latter two developments of the sheath as the *ventral lobes of the sheath* (VLSH). In the two species groups where the ventral development of the sheath is most pronounced, each protrusion is reinforced by a sclerotized plate, the *process of the ramus of the cingulum* (PRC in Fig. 1 C-E). In the Psolus Group this process can be observed readily even in dried specimens. The homologue in dry material of the Humphreysii Group is obscured by the more heavily

sclerotized lobes of the sheath, but is easily seen in cleared genitalic preparations.

The ventral lobes of the ectophallic membrane are well-developed. Each lobe bears a distinctive, rather large sclerotized plate (SVL in Fig. 1). These plates are elongate obovate in shape, are usually decidedly granular papillose, and lie on the under side of the genital mass just below and lateral to the *ventral cleft* of the phallotreme.

The *ramus of the cingulum* is broad in the Crassus Group (RC in Fig. 1 A and B). In the Psolus and Humphreysii Groups, it is narrower and bears a *process* (PRC in Fig. 1 C-F) which functions as a support for the ventral development of the sheath (VLSH in Fig. 1 C-F). In all groups, the ectophallic membrane extends beyond the ends of each ramus to form a *ventral lobe of the ramus of the cingulum* (VLRC in Fig. 1). Each of these lobes bears a more or less strengthened disc, bordered by a membranous margin. The margin folds back to become continuous with the endophallic membrane of the phallotreme to produce a *ventral cleft* (VC in Fig. 1).

In order to interpret the significance of the variation of aedeagal parts, a number of measurements were made of the dorsal and ventral valves, of certain relationships between these valves, and of their relation to the point of origin of the ventral lobes of the sheath. In the Psolus and Humphreysii Groups which have well-developed ventral lobes of the sheath, a distinct angle or *notch* occurs on the lateral side of the aedeagus at the base of the visible portion of the ventral valve. This notch (point X in Fig. 1 C and E) has been used as a reference point. In the Crassus Group the notch is absent and we have used for the purposes of measurement a morphologically equivalent point (X in Fig. 1 A).

Measurements taken were:

Length of Aedeagus.— The length of that portion of the ventral valve not covered by the sheath, the distance from X to the distal tip of the valve, taken in lateral or dorso-lateral view.

Width of Aedeagus.— Ratios of the length to the width of the aedeagus were made for each of the three groups of species. Owing to the different shapes of the internal genitalia, it was necessary to select different reference points for aedeagal width in the groups, as follows: Psolus Group, maximum dorsal width of the dorsal valves; Crassus Group, maximum dorsal width of the dorsal valves;

Humphreysii Group, width of the ventral lobes of the sheath, taken in ventral view.

Length of Exposed Portion of Ventral Valves.— The distance from the distal tip of the dorsal valves to the distal tip of the ventral valves,

taken in dorsal view.

Length of Free Lobes of Dorsal Valves.— The distance from the distal terminus of the fusion of the dorsal valves to the tips of the valves, taken in dorsal view.

POECILUS
A — B

E — F
H. HUMPHREYSII

C — D
PALOVIRIDIS
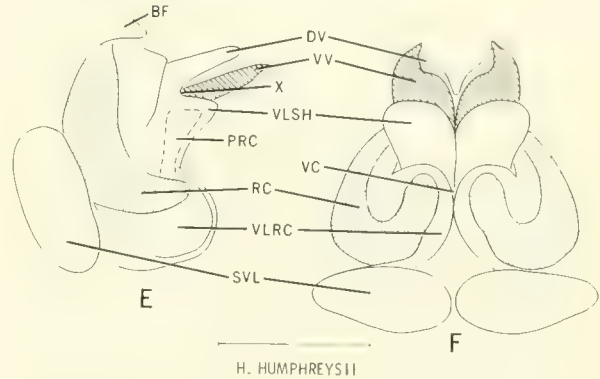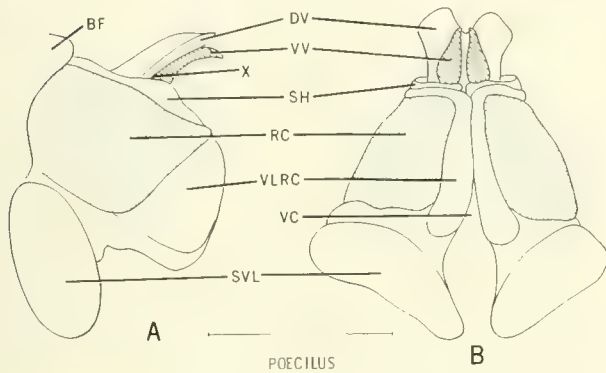
Figure 1. Semi-diagramatic drawings of the three types of concealed male genitalia found in the species groups of *Barytettix*. Scale below each figure equals 1 mm. A, C, E. Lateral views. B, D, F. Ventral views.

A, B.   *poecilus.* México: Sinaloa, El Venadillo
C, D.   *paloviridis.* México: Sinaloa, 39.9 mi SE Culiacán
E, F.   *humphreysii humphreysii.* México: Sonora, 17.7 mi N Imuris

Symbols used in figures:
BF	—	basal fold
DV	—	dorsal valve
PRC	—	process of ramus of cingulum
RC	—	ramus of cingulum
SH	—	sheath
SVL	—	sclerite of ventral lobe of ectophallic membrane
VC	—	ventral cleft
VLRC	—	ventral lobe of ramus of cingulum
VLSH	—	ventral lobe of sheath
VV	—	ventral valve
X	—	the notch
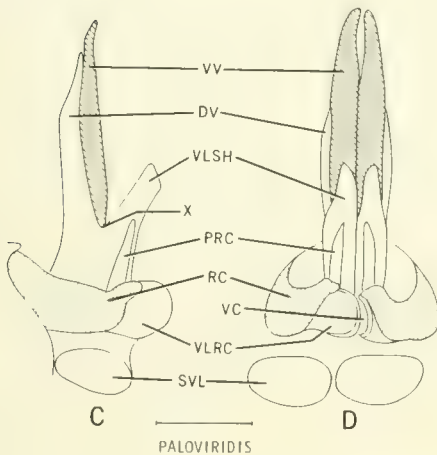
THE FEMALE INTERNAL COPULATORY
ELEMENTS

TERMINOLOGY.— Kevan, Akbar, and Chang (1969) presented a lengthy and useful summary of the literature on concealed copulatory structures in acridoid insects and, in an attempt to homologize the various copulatory elements in both sexes, have proposed a number of changes in terminology. We follow the terminology for the female elements essentially as proposed by Gregory (1965) [see Figures 2 and 16], because his study dealt with a single species of the Acrididae and, in a sense, his terminology is therefore more relevant to our work. Further, we are at

variance with Kevan, Akbar, and Chang with regard to the terms "proximal" and "distal," preferring to consider "proximal" as pertaining to the point of origin or base of the receptaculum seminis, rather than from the viewpoint of an anterior-posterior relation. Since the receptaculum seminis is essentially a diverticulum we consider the spermatheca to be distal. Thus, several terms proposed by Kevan, Akbar, and Chang are not appropriate to our use. We agree with these authors, though, in that less confusion will exist if the term "spermatheca" is limited in use. We

use their proposed term "receptaculum seminis" for the entire organ generally referred to as the "spermatheca."

In the receptaculum seminis of females of *Barytettix* there is a variously elongated enlargement (BC in Figs. 2 and 16) of the spermathecal duct between the aperture of the duct and the orifice of the thick tube[3]. The aedeagus is fitted into this chamber during copulation. This being true, we refer to this enlarged portion of the receptaculum seminis as the "bursa copulatrix," or, sometimes, simply as the "bursa."

THE RECEPTACULUM SEMINIS.— Our dissections were based upon females selected from localities which we considered critical, and, even though we have not been able to determine the limits of variation, we have little reason to believe that the results of our studies will be greatly modified by an examination of a larger number of specimens. This conclusion is based upon our experiences with intrademe variation in the acridoids and upon the findings of Slifer and Randell. Slifer (1940a:3), investigating the distal end of the receptaculum seminis, and Randell (1963:248), working with the female copulatory armature, both found the intra-specific range of variation to be minor in the acridids which they studied.

Other than the comments of Slifer (1940b: 209), who figured and described the condition found in several species of acridids, there is little comparative information in the literature regarding the functional shape and structure of the proximal portions of the spermathecal duct. Berlese (1882) and Fedorov (1927) noted dilation in this portion in some species. Slifer (1940b:209) pointed out that in those acridids ". . . which possess a spermatheca with both an apical and a preapical diverticulum usually have the proximal end of the duct conspicuously en-

[3]Kevan, Akbar, and Chang (1969:248) refer to this region as the "valve of spermathecal duct" and define their term as ". . . a small, thickened, often locally sclerotized area (or areas) within the orifice of the spermathecal duct . . . ." Gregory (1965) stated that in *Locusta* " . . . close to the spermathecal aperture the ventral wall bears a triangular, sclerotized plate (tsp)." In some species of *Barytettix* this region of the receptaculum seminis is variously sclerotized at the distal end. Our interpretation of the function of these hardened areas is that they serve to more effectively bring the distal portions of the aedeagus into precise apposition with the orifice of the thick tube, thus producing a continuous channel from the male spermatophore sac to the female spermatheca. Our dissections indicate that these plates also serve as the terminal point of aedeagal insertion. How these sclerotized areas could function as a valve capable of closing off the entrance to the thick tube is not clear.

larged, grooved above and its walls much thickened." Packard (1878) termed this region of the duct the "bursa copulatrix," and Paoli (1937) and Gregory (1965:40) both refer to this portion as the "thick tube."

The chief differences between the internal genitalia of the females of *Barytettix* lie in the shape and diameter of the thick tube, and in modifications of the bursa copulatrix (BC in Figs. 2 and 16). The more distal parts of the receptaculum seminis, the constricted tube, the vestibule, and the diverticulae, are typically melanoploid and are rather similar from taxon to taxon (Figs. 2 and 16). In all taxa, an elongate shallow concavity exists in the roof of the genital cavity (GC in Fig. 2). This concavity is indicated by dashed lines in Figures 2 C, 17 D-F, and 18 G-L. It extends from the opening to the exterior between the ventral ovipositor valves (X in Fig. 2 C), to near the center of the area encompassed by the basivalvular sclerites (ABS in Figs. 2 B and 16 A). Here the concavity forms an opening (the spermathecal aperture of Gregory, 1965) into the bursa extending above and distally. The channel is open ventrally, has a broad, gently arched roof, and bears a shallow reinforced concavity on each lateral surface. The amount of reinforcement of the lateral surfaces is interspecifically variable. The positioning of the genital components in the cleared tips of the abdomens of a mating pair of *Barytettix* suggests that the channel serves to orient the aedeagus during insertion into the bursa.

A cleared receptaculum seminis is flexible, resilient, and cartilaginous-like in texture. When any part is displaced, it will spring back into position when the cause of the tension is removed. This resiliency is much more noticeable in the bursa and proximal portions of the thick tube than in the more flexible remainder of the organ.

The walls of the bursa are capable of considerable expansion or stretching. This is most evident in the lateral and dorsal surfaces of the lumen which may be folded or pleated (note cross-sections of bursa in Fig. 18 L). A bursa which is minimally reinforced with sclerotin is rather feebly pleated and probably is subjected to minimal stretching and stress during mating (Figs. 16 A and E, 17). Similarly, in those species where a little more than minimal stress appears to be involved, the reinforced areas are smooth, or folded only laterally. However, per-

tinent areas are pleated in bursae which must accommodate for an aedeagus of greater diameter, as well as for the stress of aedeagal insertion (Figs. 16 C, 18 L). Smooth and pleated areas of the lateral and dorsal walls, and, additionally in some species, a reinforcement in the distal portions of the ventral wall, all may occur in the same bursa. These reinforced areas lend strength and rigidity to the walls which undergo the greatest stress as the aedeagus is inserted, and serve to aid in aligning the aedeagus correctly. The pleatings and resiliency of the bursa walls permit the bursa to expand to receive the aedeagus and to ensure a close "hand-in-glove" fit, thus further ensuring proper alignment of the orifice of the phallotreme and the opening of the thick tube.

H. HUMPHREYSII

B

PALOVIRIDIS

C

PALOVIRIDIS
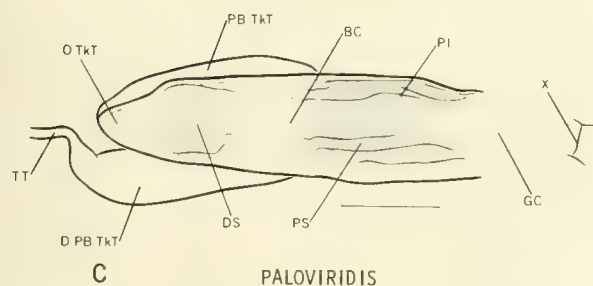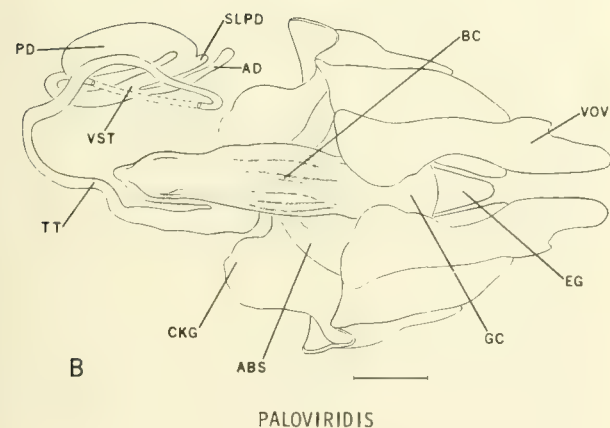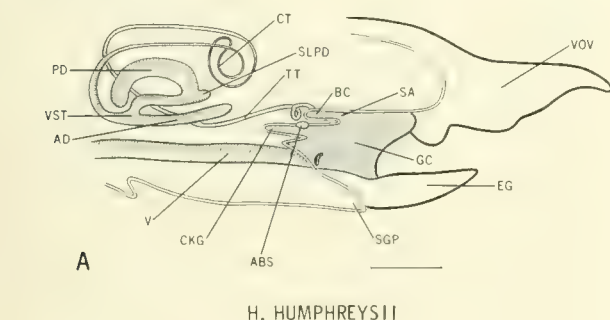
TAXONOMIC VALUE.— In certain groups of the Acridoidea the structure of the elements of the male concealed genitalia are sufficiently varied so that these parts are used taxonomically at the specific and intraspecific levels. In these same groups, the female internal genitalic elements have been considered to be less diverse, and, as pointed out in the lengthy summary of Kevan, Akbar, and Chang (1969), less reliance has been placed on them as taxonomic tools. Few studies have involved the entire receptaculum seminis, and we are not aware of any study of this organ on a comparative specific basis. As a result, we have been quite surprised to find that in *Barytettix* the receptaculum seminis affords diagnostic features of unusual value at several taxonomic levels. Furthermore, we feel the pattern of variation of female genitalia in this genus forms an integral part of the primary evidence for genitalic reproductive isolation, a theory discussed in a later section (page 93).

MEASUREMENTS.— In our study we have indicated relative size of the bursa copulatrix by using a length to width ratio based upon the distance from the distal tip to the distal edge of the

Figure 2. Female internal copulatory elements in *Barytettix*. Scale below each figure equals 1 mm.

A. *humphreysii humphreysii*. Semi-diagramatic, parasagittal section of ventral portion of tip of female abdomen. México: Sonora, Copete Mine, 30 mi E Carbó (ANSP)
B. *paloviridis*. Receptaculum seminis and ventral ovipositor valves, dorsal view. Topotype. México: Sinaloa, 2.5 mi NW bridge over Río Culiacán at Culiacán. I. J. Cantrall and T. J. Cohn, 1961 No. 56
C. *paloviridis*. Bursa copulatrix, dorsal view (same data as for B.)

Symbols used in figures:

ABS	—	anterior basivalvular sclerite
AD	—	apical diverticulum
BC	—	bursa copulatrix
CKG	—	Comstock-Kellogg Gland
CT	—	constricted tube
DPBTkT	—	dilation proximal bend of thick tube
DS	—	distal sclerite of bursa copulatrix
EG	—	egg guide
GC	—	genital chamber
OTkT	—	orifice of thick tube
PBTkT	—	proximal bend of thick tube
PD	—	preapical diverticulum
PL	—	pleats
PS	—	proximal sclerite of bursa copulatrix
SA	—	spermathecal aperture
SGP	—	subgenital plate
SLPD	—	secondary lobe preapical diverticulum
TT	—	thin tube
V	—	vagina
VOV	—	ventral ovipositor valve
VST	—	vestibule
X	—	distal edge of membrane connecting ventral ovipositor valves

opening from the genital cavity into the bursa (dashed transverse line in Figs. 2 C, 17 D-F, 18 G-L), and a maximum width between these points of reference.

THE SYSTEMATIC POSITION OF THE CONALCAEA COMPLEX

In recent years much progress has been made in the stabilization of higher categories in the Acridoidea. Roberts (1941), Dirsh (1956, 1961), and Uvarov (1966a) have contributed and characterized classifications at the subfamilial and familial levels, and Dirsh (1966) established several superfamilial taxa. Rehn (Rehn and Randell, 1963) has presented a lengthy, although somewhat biased, account of the historical development along these lines, particularly as it pertains to a single supertribe, the Melanoplini.

Much of the evidence for the association of various genera into higher categories has been derived from the study of the internal genitalia of the male. Although Uvarov (1966b) gave no specific reasons for his action, we postulate that his establishment of the subfamily Melanoplinae is based largely on the presence of a sigmoid flexure between the aedeagus and the endophallic plates in *Catantops* (Catantopinae) as compared to a constricted point of articulation between these structures in *Melanoplus* (Melanoplinae). This difference between *Catantops* and *Melanoplus* was shown by Roberts (1941:222-223).

Rehn and Randell (1963:7) gave a number of ". . . chief characters . . ." which they used to characterize their supertribe Melanoplini (probably = Melanoplinae of Uvarov, 1966b). All but one of these features are so variable that it is not possible to utilize them singly in the assignment of specimens to a supertribe. One feature, a constricted point of articulation between the aedeagus and the endophallic plates, is unique. On the basis of this genitalic characteristic, *Barytettix*

and *Conalcaea* were considered components of the Melanoplini.

Similarly, characteristics used by Rehn and Randell (1963:8-10) to differentiate tribes are so variable and so overlapping that we are unable to associate any species of *Barytettix* with a specific tribe. Fortunately Rehn and Randell presented in a list (1963:10-12), their assignment of genera to various tribal groupings. Since a cluster of characters appears to be needed to associate a given genus with a given tribe or generic group, these authors, in their generic assignments, undoubtedly depended heavily upon character similarities, as well as subjective evaluation grounded upon the historical categorization of a taxon, and upon Rehn's vast experience with the Orthoptera. Their assignment of numerous genera as being "atypical" suggests that their characterizations are not refined to the point where specific characters are unique for a given category. Numerous authors (*vide supra*) have pointed out the generic heterogeneity of the Catantopinae and of the Melanoplinae. The classification of Rehn and Randell was, in their words, ". . . admittedly, a tentative one, . . ." (1963:6), and, on this basis, they must be credited with making some progress. Nevertheless, much heterogeneity is still apparent in their hierarchy. This is evident in their placing *Barytettix* and *Conalcaea* as "atypical" components of the tribe Melanoplini (=Melanoplinae of Uvarov, 1966b).

Barytettix, *Conalcaea* and two undescribed genera have a number of characteristics in common. The four genera form a rather cohesive unit which we propose as the tribe Conalcaeini.

Conalcaeini new tribe

In western México, in the northern portions the area occupied by the Conalcaea Complex, the taxa assignable to the genus *Conalcaea* are montane, whereas those assignable to the genus *Barytettix* occupy the lowlands. Southwardly both of these genera overlap undescribed generic counterparts. All of these we consider as belonging to the tribe Conalcaeini. The species of

these genera share numerous characteristics listed below.

1. A rather stocky or robust body.
2. A pronotum gradually widening caudad and with the posterior margin broadly emarginate.
3. Tegmina lateral, elongate-lobate, with

rounded apices (Frontispiece).

4. Male supra-anal plate trigonal, with rounded apex and usually with a single tooth or sharp projection dorsally on each medio-lateral surface (Figs. 8 A-B).

5. Furculae represented by short, rounded lobes (Figs. 8 A-B).

6. Cerus shape based on a short falcate pattern with the disto-dorsal margin variously enlarged, distally and usually dorso-distally incurved (Fig. 6).

7. Subgenital plate conical (Figs. 8 H, 15 H).

8. Sheath of the phallus complex and involved in the formation of the dorsal valve of the aedeagus.

9. Presence of striking, much enlarged, appressed and usually sclerotized ventral lobes of the ramus of the cingulum (VLRC in Fig. 1).

10. Presence of an exceptionally well-developed pair of sclerotized areas in the ventral membrane of the phallic mass (SLV in Fig. 1). These obovate areas lie in the ectophallic membrane on each side and below the phallic mass, the ventral portions near one another, thus forming, in caudal view, a broad broken U-shaped reinforcement. They are variously sclerotized and papillose. Their function is unknown, although we surmise that they serve to aid in holding the male genital mass in position during copulation. We have found them in all of the species of the Conalcaeini.

Genus *Barytettix* Scudder

DIAGNOSIS.— The genus *Barytettix* is related most closely to *Conalcaea*. The features differentiating the two genera are listed in Table 1.

BARYTETTIX AND OTHER MELANOPLINE GENERA IN WESTERN MÉXICO.— Within the range of *Barytettix* there are a number of described and undescribed short-winged grasshoppers which might possibly be confused with *Barytettix*. Several of these are quite distinctive and, in the field, offer little difficulty in recognition. Others approach *Barytettix* in one characteristic or another.

As noted above, species of *Conalcaea* are readily distinguished from those of *Barytettix*. The remaining taxa of Conalcaeini are as yet undescribed, but can be recognized from *Barytettix* by having the habitus and color pattern of a *Conalcaea*, or in lacking the distinctive *Barytettix* black and yellow blotch on the lateral lobes of the pronotum. In these forms the disto-lateral ends of the lophi smoothly join the posterior projections of the lateral plates of the epiphallus without creating the notch characteristic of *Barytettix* and *Conalcaea*. Further, the sheath caudad of the ventral aedeagal valves is complexly convoluted.

Other than the taxa of the Conalcaeini there are few short-winged species which bear even a superficial resemblance to *Barytettix* except for the genus *Sinaloa*. The general body habitus, shape of the pronotum, and shape of the tegmina of species of this genus are similar to those characteristics in *Barytettix*. Even color and color pattern tend to resemble those of green individuals of *Barytettix*. This is particularly true of *Sinaloa nitida* (Scudder) where the resemblance is striking. However, the mainland species of *Sinaloa* before us[4] are readily separated from the species of *Barytettix* on the basis of several characteristics. A fastigium less protruding before the eyes than in *Barytettix* and a pronotum without humeral sinuses give specimens of *Sinaloa* a rather characteristic appearance. Elongate finger-like furculae, absence of spinules on the medio-lateral surfaces of the supra-anal plate, and a subgenital plate with a short blunt cone serve to differentiate the males of these *Sinaloa*. The presence of a proximal node on each side of the sub-obsolete longitudinal furrow of the supra-anal plate of the males of *S. behrensii* and *nitida* is also distinctive. The females of *Sinaloa* lack the deep sinus found laterally on each side of the subgenital plate of female *Barytettix*. The species of *Sinaloa* lack a mid-dorsal longitudinal light line on the abdominal segments, and the black spot on the lateral lobes of the

---

[4]*Sinaloa nitida* Scudder, *behrensii* Scudder, and *pulchella* Hebard. We have not seen *peninsulae* (Scudder) from Territorio de Baja California. The species is known from the female type described as a *Barytettix*. It was transferred to *Sinaloa* by Hebard (1917:262).

TABLE 1

DIAGNOSTIC COMPARISON OF *BARYTETTIX* AND *CONALCAEA*

Barytettix	*Conalcaea*
Colors bright and contrasting (Frontispiece): ground color green, blue, gray or brown, usually with much yellow; hind tibiae bright yellow, red, blue, or intermediates, or combinations.	Dull brown or gray, never green or blue; with little or no yellow; hind tibiae pale orange or dull yellowish.
Antennae orange.	Antennae brown.
Disc of pronotum with yellow dorso-lateral stripes; black blotch on lateral lobes usually broken with yellow lines (except in southern *nigrofasciatus* and southern *psolus* which have a continuous dark band across entire lateral lobe) and usually restricted to pro- and mesozona.	Disc of pronotum brown; lateral lobes with a usually continuous dark band from cephalic to caudal margin.
Metanotum and abdomen usually with a yellow medio-longitudinal band (absent in *terminalis* and some southern *poecilus*).	When present, yellow medio-longitudinal band restricted to abdomen.
Tegmina usually unicolorous, rarely darker below, then never sharply divided in color.	Tegmina almost always sharply divided into a lighter upper half and a lower darker (usually blackish) half.
Hind femora with thin, black, dark green, or gray lines on ventral outer and dorsal carinae (except in *terminalis* and some *poecilus*).	Hind femoral carinae brown and not darker than the rest of femur.
Nymphal pronotum (Frontispiece) (nymphs of *contilus contilus* and *c. hiscatus* not available) with a broad median whitish or yellow stripe bordered by broad dark or usually velvety black stripes (except some individuals and population variants in *tridens* and *humphreysii*); stripe sometimes extending to occiput and usually only as far as second or third abdominal segment. (This pattern is unique in Mexican Melanoplinae known to us.)	Nymphal pronotum brown, or with narrow median stripe, or with a somewhat broader stripe continuing the length of the abdomen; sometimes bordered laterally with dilute brown stripes.
Pronotum transversely convex, without lateral carinae; metazona finely and densely punctate.	Dorsum of pronotum flatter, with well-defined, but not sharp lateral carinae; metazona less densely punctate, with punctations ill-defined and often sub-obsolete.
Dorsal aedeagal valve in side view, linear, without a decided lobe (Figs. 1 A, C, E).	Dorsal aedeagal valve with a lateral, lobe-like, decurved expansion covering part of lateral edge of ventral valve.
Lowland	Montane

pronotum is an unbroken stripe either running the length of the pronotum with yellow above and below, or terminating at the principal sulcus and bounded by yellow. This black or dark bar is of solid color except in females of *nitida* where flecks of yellow may occur in the black.

In the geographic area under consideration, the tyro may possibly experience some difficulty in separating the genera *Philocleon* and *Oedomerus* from *Barytettix*. *O. corallipes* Bruner has been reported from southwestern Arizona, Guaymas, Sonora, and Territorio de Baja California. The species is mottled sombre brown in appearance, and is without the conspicuous orange of the antennae, the black and yellow markings of the lateral lobes of the pronotum and the darkened upper half of the pagina characteristic of *Barytettix*. The dorsal surfaces of the caudal femora are bifasciate and the outer carinae of the caudal tibiae bear 6-7 spines instead of 8-10. The supra-anal plate of the male is without spinules, and the furculae are absent. The female subgenital plate is laterally so deeply notched as to appear W-shaped in ventral view. *Philocleon nigrovittatus* (Stal) occurs in both Jalisco and Colima. The dorsum of the pronotum of the species of *Barytettix* in this part of México is green, bordered laterally with a thin yellow line. The pro- and mesozona of this structure in *P. nigrovittatus* is longitudinally multi-striped with black and lighter colors; the metazona is marked with brick red.

Barytettix may be differentiated from any other short-winged melanopline genus occurring within its range by the conical subgenital plate and the presence of spinules on the supra-anal plate of the male, the broadly emarginate caudal margin of the pronotum, and the elongate-lobate tegmina.

GENERIC DESCRIPTION.— BODY robust, usually large; length from fastigium to tip of caudal femora: male, 20.4-39.2 mm, female, 25.3-45.2 mm. HEAD normal, not exserted; vertex feebly elevated above level of eyes; fastigium of vertex weakly sulcate, produced before the eyes, rounding smoothly to the facial carinae; facial carinae percurrent to clypeus, interspace sulcate throughout; antennae filiform, extending to about the middle of the tegmina. PRONOTUM gradually widening caudad; convex in cross-section, without lateral carinae; median carina weak to obsolete, intersected by the principal sulcus only; anterior margin weakly convex-truncate; posterior margin distinctly broadly emarginate; punctate dorsally and laterally, with the metazona decidedly and contrastingly so. TEGMINA (Frontispiece) lateral, elongate-lobate, with rounded apices; reaching about to or slightly beyond the base of the second abdominal tergite. TYMPANUM present. No known stridulatory mechanisms. MESOSTERNAL lobes rounded, well-separated. FEMORA of cephalic and middle legs moderately bullate. CAUDAL

FEMORA incrassate to moderately incrassate, lower lobe shorter than upper, slightly exceeding tip of abdomen in male. BRUNNER'S ORGAN present. CAUDAL TIBIAE terete in cross-section, without external distal spine, outer margin bearing 9 (8-10) evenly spaced spines. SECOND TARSAL joint shorter than first. PROSTERNAL SPINE well-developed; conical; bluntly acute; straight or feebly retrorse. TERMINALIA, MALE—Supra-anal plate (Figs. 8 A-B) trigonal; as long as wide to wider than long; usually with mid-distal lateral distinct spinules; usually with shoulders near tip; apex rounded, often with distal surface raised and forming a plate-like extension to the edges of the longitudinal furrow. Furculae reduced to short, rounded lobes. Cerci (Fig. 6) falcate with disto-dorsal margin variously enlarged, distally and usually dorso-distally incurved. Subgenital plate (Figs. 8 H, 15 H) distinctly evenly conical. TERMINALIA, FEMALE—Lateral margins of subgenital plate evenly rounded. Ovipositor valves normal, well-sclerotized; dorsal margins of the upper valves and ventral margins of the ventral valves dentate. CONCEALED GENITALIA, MALE (Fig. 1)—Epiphallus bridge-shaped; ancorae well-developed, tooth-shaped; lophi strongly developed, arched, disto-lateral ends separated from the posterior projections of the lateral plates by a distinct sinus[5]; oval sclerites absent. Sclerite of the ventral lobe of the ectophallic membrane highly developed into a distinct, strongly sclerotized area. Ventral lobes of the ramus of the cingulum strongly and distinctly developed, appressed and usually sclerotized. Sheath fused with the dorsal aedeagal valves, in most taxa completely covering them; ventrally converging medio-distally from the tips of the rami of the cingulum toward and under the ventral side of the ventral aedeagal valves so as to form a pair of valve-like variously sclerotized, flattened, collar-like or finger-like projections (the basal lobe of Gurney, 1951); these simple, not convoluted or folded in a complex manner. INTERNAL GENITALIA, FEMALE (Figs. 2 and 16)—Comstock-Kellogg glands present. Spermatheca with both apical and preapical diverticulae, the preapical bearing a secondary lobe. Bursa copulatrix variously developed from a small, simple, unpigmented, sack-like structure to elongate, variously sclerotized and pigmented chamber. COLORATION (Frontispiece)—Ground color yellow, yellow-brown, brown, gray, blackish, blue or green; with yellow and black stripes and markings. Antennae orange (probably always so in life), rarely brownish. Head usually with yellow post-ocular stripes. Pronotum usually with dorso-lateral yellow stripes running the entire length, or terminating at principal sulcus; remainder of dorsum monochromatic or with an obscure median yellow stripe margined with dark brown or black; lateral lobes with a black spot extending over at least the dorsal portion of the pro- and mesozona, bordered with yellow, black spot partially or completely broken on prozona by a ventro-cephalic diagonal yellow line, and often partially or completely broken on mesozona by a horizontal yellow line. Abdomen usually with a mid-dorsal yellow stripe narrowly margined with black, and usually proximally with a dorso-lateral broken yellow line or band, bordered laterad by narrow black blotches; caudal segments usually tinged with color of caudal tibiae (probably always so in life). Tegmina with yellow or yellow-brown veins, membrane black, rarely precostal and costal areas totally black. Metepisternum yellow or yellow-brown; meso- and metepimera green, black, or yellow margined with black. Caudal femora with carinae black, or a shade of brown or green darker than lighter portions of the femur; genicular areas usually tinged with the color of the caudal tibiae, with black or dark lunae; dorsal half of pagina usually darkened, often contrasting strongly with a lighter colored ventral half. Caudal tibiae brightly colored, yellow, orange, pink, red, reddish-purple, purplish-blue, or blue; spines black tipped. Tarsi concolorous with distal portion of tibiae. Nymphs usually and distinctively marked with three broad stripes on dorsum of pronotum: the median yellowish,

---

[5]This notch, characteristic of the epiphallus, is shared by the species of *Conalcaea*.

the laterals velvety black.   CHROMOSOMES–Prof. B. John, (*in litt.*) Department of Zoology, The University of Southampton, who examined the chromosomes of four or five individuals each of *humphreysii humphreysii, tridens, paloviridis, psolus, contilus dicranatus, contilus similis, nigrofasciatus, poecilus,* and *terminalis,* indicated that ". . . all of them had the same chromosome number, 2n = 23 male (XO), . . ." and that ". . . all had a marked pattern of chiasma localization with chiasmata predominantly occurring at the distal ends of the chromosomes . . . at least in males."

THE SPECIES GROUPS OF *BARYTETTIX*
AND TABLES FOR THE
IDENTIFICATION OF SPECIES

It would be easy for us to state our conclusions on the grouping of species within *Barytettix* and to justify these by citing carefully selected data.   This is the traditional method, but it has serious drawbacks.   It tends to obscure many data, and it prevents the independent assessment of the reliability of those groupings and the possibility of alternative ones.   The most objective method would be some sort of numerical taxonomic treatment.   In this genus, however, we have encountered much difficulty in coding character states and in handling the very extensive geographic variation in many of the species. Furthermore, the coding itself makes rapid examination and assessment of the data almost impossible.   We have therefore chosen a compromise method.   In Tables 2 and 3 (p. 24) we list most of the morphological and color characteristics of all the species, and present below a discussion of the correlations seen in the tables and the results of grouping the species in different ways.   We have not included certain characteristics present in only one species, others which are intraspecifically highly variable, a few which require detailed description, and those in which the differences between species are too slight to describe adequately in abbreviated form.

These tables can also be used as tabular keys for identification.   Our reasons for substituting tables for keys are given in the Methods section. Any character or combination of characters may be used in any sequence for identification, but the characters are so arranged that the first three and the tenth (phallotreme), used together, will serve to identify any male of the genus.   In addition, we have used bold-face type to designate distinctive and easily recognizable conditions. Without dissection most females cannot be identified to species, but the possibilities can be limited to two or three by color characteristics.

The most obvious correlation in the tables is that of the characters of *poecilus, crassus* and *terminalis.*   Of the 12 morphological characteristics shared by these species, three of the aedeagus and four of the bursa are distinctive. These species are similar in almost all other genitalic and color characteristics, although the same features may also be found in other species. *Terminalis* differs from the other two species in five characters.   In each case, the condition in *terminalis* resembles no other species, or it differs only slightly from conditions in *crassus* or *poecilus.*   The three listed differences between *crassus* and *poecilus* also are small differences in degree and not of kind.   Other differences among these species listed in Table 4, p. 26, are either unique or slight.   There is little question that *poecilus, crassus* and *terminalis* represent a cohesive unit which we name the Crassus Group.

Of the remaining taxa, *contilus, psolus, nigrofasciatus,* and *paloviridis* share an unusually elongate aedeagus and associated female bursa, strap-shaped ventral valves, distinctive ventral lobes of the sheath, and a ventro-caudal orientation of the proximal bend of the thick tube.   Among these species there is a mosaic of similarities in several other distinctive features (see also Table 6, p. 34, and Table 7, p. 38).   Thus, *psolus, nigrofasciatus* and *paloviridis* share distinctively long and dilated thick tubes, a similarly very elongate aedeagus, and an almost invisible phallotreme, whereas *contilus, nigrofasciatus* and *psolus* share a distinctive color pattern, semicircular dorsal valves (in cross-section), as well as two distinctive features of the ventral lobes of the sheath (at least as variants in *psolus*).   *Psolus* and *nigrofasciatus* also share with one of the *contilus* subspecies (*tectatus*) almost identical sclerotizations of the bursa.   Both *contilus* and *psolus* have lateral apices of the dorsal valves, and *nigrofasciatus,* some *paloviridis,* and *contilus tectatus* share a distinctive hump on the dorsal valves.

Paloviridis and *contilus* show specific similarities to other species.   The color and pattern of *paloviridis* is identical to those of *poecilus* and *terminalis* (except for the lack of an abdominal stripe in the latter), and to the green geographical

variant in *h. humphreysii. Paloviridis* shares no other characters with *poecilus* and *terminalis,* and very few with *h. humphreysii.* In the case of the listed similarity to *h. humphreysii* the excision of the dorsal valves is between acute median teeth in *humphreysii,* but between the two simple free lobes in *paloviridis.* Otherwise those two species are similar in only two general features, the dorsal position of the dorsal valves (as in the Crassus Group also), and their narrowly rounded apices (in some of the geographical variants in *humphreysii* which usually also have median teeth, unlike *paloviridis). Contilus* is similar to *h. cochisei* in the broadly open phallotreme with more or less parallel dorso-lateral margins, and in the short proximal bends of the thick tube of the female. However, the ventral valves are otherwise rather differently shaped and the thick tube has a different orientation in the two species. The similarities which *paloviridis* and *contilus* bear to the Crassus Group and to *h. humphreysii* and *h. cochisei* do not outweigh the more numerous and distinctive similarities they bear to *psolus* and *nigrofasciatus.* We therefore designate *contilus, psolus, nigrofasciatus,* and *paloviridis* as members of a second species group, the Psolus Group.

The remaining taxa, *tridens, h. humphreysii,* and *h. cochisei,* together share no highly distinctive characteristics, but are generally similar in almost all features. Furthermore, *tridens* is almost identical to the southernmost and adjacent *h. humphreysii* populations in most characters except the ventral lobes of the sheath, details of the ventral valves, and the color of the northern colonies. Even in these characters, there is general similarity to at least some *humphreysii* colonies, and little similarity to any other species. *Tridens* and southern *humphreysii* also share the distinctive strongly incurved and distally greatly expanded cercus. *H. cochisei* is almost identical to the adjacent northern *h. humphreysii* populations in cercus, ventral lobes of the sheath, thick tube of the female, ground color, color pattern, geographic trends in color and pattern, and in some genitalic features (Table 15, p. 79). The *humphreysii* populations south of Hermosillo have ventral valves which are generally similar to those of the adjacent *cochisei* populations (Figs. 11 B and G). Where *cochisei* differs strongly from *humphreysii* in the dorsal valves, it shows no obvious similarity to any other species. Nor is the more elongate aedeagus or bursa of *cochisei*

more similar to *contilus* except in the broadly visible lateral walls of the phallotreme. As noted above, the ventral valves which contain the phallotreme are of a different shape in *cochisei,* and in this they are more similar to *humphreysii.* That subspecies also has a broadly open phallotreme, at least in the northern populations, but it is obscured by the more closely set dorsal valves. Thus, *tridens, humphreysii* and *cochisei* are much more closely similar to one another than any are to other species, thus qualifying them for designation as the third species group which we name the Humphreysii Group.

The decision to treat these clusters of species as groups rather than distinct genera was based on a number of considerations. A genus is an arbitrary unit in nomenclature and can reflect either a typological approach or one of biological continuity and relationship. All the species here considered have geographic cohesiveness in distribution, are all readily recognizable as being very similar in size, body contour, wing shape, wing length, and color pattern, as well as several features of the male external copulatory armature. The elements of the concealed male and the internal female genitalia which seem to differ so strongly one from another can all be readily homologized and are without doubt derivatives one from another, part by part. We feel that an appreciation of these phylogenetic relationships would be seriously obscured by the recognition of additional generic entities.

THE CRASSUS GROUP

Occupying the southern portion of the range of the genus are a group of populations which are similar in all bursal, and almost all aedeagal and color features. Several of the shared aedeagal and bursal characteristics are distinctively different from all other *Barytettix* species. These southern populations thus form a morphologically and geographically cohesive group within the genus.

The group comprises a widespread form in Sinaloa and Nayarit, *poecilus,* and two geographical isolates, *crassus* in southern Baja California, and a new species, *terminalis,* in coastal Jalisco near Colima. Although these might well be treated as the subspecies of a polytypic species, we think that the differences between them are numerous enough, and some are distinctive enough, to indicate that they represent the com-

ponents of a biological superspecies. Furthermore, we find no tendency toward the distinctive features of either *crassus* or *terminalis* in the widespread and geographically variable *poecilus*, suggesting a longer rather than a shorter period of isolation.

We consider it best to treat the marked geographic variation in *poecilus* descriptively rather than using it to erect subspecies. One of four geographically variable characters in *poecilus* is discordant with the other three. Of the remaining three which are concordant, one exhibits additional variation not shown by the others, and two show different degrees of intrapopulation variation. We believe that designation of subspecies might obscure this biologically significant pattern.

The three species share the characteristics listed below which are unique within the genus.

1. Dorsal aedeagal valves (Figs. 7 B, D, F; 8 C): strongly fluted longitudinally, enlarged disto-laterally (when pressed flat), disto-lateral portions up-turned, free lobes short, making valves appear merely notched medio-distad.
2. Ventral aedeagal valves with a usually well-developed, oblique ridge on ventral surface (Figs. 8 D-E).
3. Ventral valves strongly curved downward or outward (Figs. 7 B, D, F).
4. Ventral lobes of aedeagal sheath short, forming only a brief collar beneath ventral valves (Fig. 7).
5. Ramus of cingulum well-developed disto-ventrad, thus reducing lobes of sheath to a collar (Fig. 7).
6. Bursa copulatrix short, the width about two times the length (Figs. 17 A, D).
7. Thick tube of receptaculum seminis arising dorso-laterally, and proceeding dorso-cephalad, wide at origin and immediately beyond, proximal bends much longer than bursa (Figs. 17 A, D).

The following characteristics, shared by all three species of the group, are also occasionally found in the Humphreysii or Psolus groups.

1. Ground color always bright green (possibly olive or brownish in *crassus*) (Frontispiece).
2. Dorso-lateral yellow pronotal stripes extremely narrow (possibly absent in some individuals, but this may be the result of poor preservation) (Frontispiece).

3. Bursa copulatrix triangular, weakly sclerotized (Figs. 17 A, D).

Table 4 summarizes the differences between the three species of the Crassus Group. Characteristics in bold-face type are more distinctive and easily recognized, and may serve as key characteristics. To distinguish any of the three species from all other species of the genus on the basis of color alone, see Table 3, p. 25, and Table 5, p. 28.

Barytettix poecilus (Hebard)
Frontispiece, Figs. 1 A-B; 6 S-X; 7 A-B; 8 A-E;
16 A-B; 17 A-D

Cantrall has determined that Venvidio as recorded by Hebard is a misspelled transliteration of Venadillo, a small village 6 mi N Mazatlán Cathedral, and not near Los Mochis as surmised by Gurney (1951:302). This determination was based on a study of the correspondence of the collector, J. A. Kusche, the localities of collections made within a few days of dates when he was known to have been at El Venadillo, and the distribution of species collected by Kusche at El Venadillo.

DIAGNOSIS.— Males of *poecilus* may be distinguished from all other *Barytettix* by the combination of an invariably green ground color, down-curved ventral aedeagal valves (Fig. 7 A), and a moderately deep, V-shaped excision of the dorsal aedeagal valves (Figs. 7 B, 8 C). Females may be distinguished from all species other than *crassus* and *terminalis* by the combination of a green ground color, short bursa copulatrix and thick, dorso-lateral thick tube. From *terminalis*, both males and females differ in the dark carinae of the femora, the frequent presence of a dark paginal stripe, and a yellow mid-dorsal abdominal stripe. From *crassus*, apparently only those females lacking paginal or abdominal stripes, or possessing blue tibiae may be distinguished, although the uniformity of alternative color characteristics of *crassus* is as yet unknown because of poor preservation of material before us and the small number of localities from which the species is known. See Table 4 for other comparisons of the species of this group.

TABLE 2

GENITALIC CHARACTERISTICS IN *BARYTETTIX* SPECIES
(Numbers and letters in parentheses refer to figures; bold-face type indicates easily recognizable, "key" characteristics.)

	poecilus (p.24)	*crassus* (p.30)	*terminalis* (p.31)	*tridens* (p.84)	*h. humphreysii* (p.66)	*h. cochisei* (p.77)	*contilus* (p.37)	*psolus* (p.44)	*nigrofasciatus* (p.47)	*paloviridis* (p.51)
MALE GENITALIA										
AEDEAGUS										
GENERAL SHAPE	[———————— Wider than long (p.14 and Figs. 1 B, 1 F) ————————]						[———— Much longer than wide (p.14 and Fig. 1 D) ————]			
Length/width	0.76 – 0.88	0.67 – 1.0	0.75 – 0.90	0.48 – 0.63	0.57 – 0.84	0.74 – 0.87	1.6 – 1.9	2.6 – 3.0	2.6 – 2.7	2.2 – 2.9
VENTRAL LOBES OF SHEATH	[———— **REDUCED TO NARROW COLLAR** ————] (1 A–B)			Laterally narrow lobed, U-excised (12 O–S)	[———— Truncate or medially ————] lobed, V-excised (1 E–F; 12 A–N)		[———— **PRODUCED, NARROW, APPROXIMATE** ————] (1 C–D)			
DORSAL VALVES										
Median excision between free lobes	V-shaped, moderately deep (7 B; 8 C)	Very broadly V-shaped, shallow (7 D)	Narrowly V- or U-shaped, moderately deep (7 F)	Narrowly U-shaped, deep or shallow (10 S–T)	Variable: V- to narrowly U-shaped; deep (10 F–R)	Broadly U- or V-shaped, deep (10 A–E)	Variable: narrow U-shaped proximad, variable distad; deep (14 A–E)	Broad distad, narrow U-shaped proximad; deep (14 G)	V-shaped, deep (14 H)	Narrow U-shaped, deep (14 F)
Projection on mesal margin	[———— None ————] (7B, D, F; 8 C)			Aciculate or acute (10 S–T)	None, obtuse, or acute; near middle (10 F–R)	None or obtuse; near base (10 A–E)	None, lobate or acute produced; at middle (14 A–E)	[———— None ————] (14 F–H)		
Apex or disto-lateral projection	Broadly rounded or rectangulate; dorsal (7 A–B)	Broadly rounded-truncate; dorsal (7 C–D)	Broadly rounded; dorsal (7 E–F)	Elongate-acute; dorso-lateral (10 S–T)	Broadly rounded to elongate-acute; dorsal to dorso-lateral (10 F–R)	Narrowly acute or narrowly rounded; dorso-lateral (10 A–E)	Narrow or broad; lateral (13 E; 14 A–E)	Broadly rounded; lateral (13 C; 14 G)	Narrowly rounded; dorso-lateral (14 H; 15 E)	Narrowly rounded; dorsal (13 A; 14 F; 15 A–D)
Cross-section (medio-distal)	[———— **W-SHAPED ABOVE** (dry preparation) ————]			Slightly convex above to turned-up edges, or concave	Moderately to slightly convex above	Slightly convex above	Semi-circular above, sometimes slightly flared	Semi-circular above	Semi-circular above, often flared distad	Strongly convex above, flaring distad
VENTRAL VALVES:										
Attitude	[———— **DOWN-CURVED** ————] (7 A, C)		**OUT-CURVED** (7 F)	Broadly incurved (11 N–P)	Broadly incurved (Tezopaco-straight) (11 E–M)	[———— Straight or slightly incurved ————] (11 A–B; 14 I–P; 15 F–G)				
General shape	[———— Gently tapering distad ————] (7 B, D, F; 8 D–E)			Moderately tapering distad (11 N–P)	Moderate to strongly tapering distad, some with strong proximal shoulders (11 E–M)	Strongly tapering distad, strong proximal shoulders (11 A–B)	[———— Strap-shaped ————] (and often gently tapering distad) (14 I–P; 15 F–G)			
Apices	[———— Blunt ————] (7 B, D; 8 D–E)		Briefly acute (7 F)	Sharp-acute or **ACICULATE** (9 F; 11 N–P)	**ACICULATE** (Tezopaco-sharp-acute) (11 E–M)	Acute or narrowly blunt (11 A–B)	[———— Briefly acute, or narrowly blunt ————] (14 I–P)			
Visibility of lateral walls of phallotreme (from above)	[———— Invisible (obscured by dorsal valves) ————] (7 B, D, F, ventral view)			[———— Broadly to narrowly visible ————] but usually narrowly obscured by dorsal valves (8 G)		[———— **BROADLY VISIBLE** ————] (8 F; 14 A–E)	Narrowly visible distad (14 G; 15 R)	Narrowly visible (14 H)	Invisible or narrowly visible distad (14 F; 15 P–Q)	
Oblique ridge on ventral surface proximad	Weakly to not projecting laterad (7 B, 8 D–E)	Strongly, roundly projecting laterad (7 D)	Angularly projecting laterad (7 F)	[———— Absent ————] (but swellings and excavations may be present)						
CERCUS										
Distal enlargement	Slight (6 S–X)	Weak (6 R)	Moderate (6 Q)	[———— Moderate to strong (6 B–P) ————]		Moderate (6 A)	Weak to moderate (6 FF–JJ)	[———— Weak or not at all ————] (6 Y–EE)		
Incurvature	[———— Weak ————] (15 H)		Moderate	[———— Moderate to strong ————] (8 H)		Moderate	[———— Weak ————] (15 H)			
FEMALE GENITALIA										
BURSA COPULATRIX										
General Length	[———— Short ————]						[———— Very long ————]			
(Length of bursa/ length of pronotum)	0.04	0.04	0.04	0.08	0.05	0.11	0.27 – 0.35 (– 0.42?)	0.50	0.54	0.42
Apex (dorsal view)	[———— Triangular (17 A) ————]			[———— Truncate (17 E) ————]		Triangular (17 F)	[———— Rounded (18 G–J) ————]		[———— Rounded-triangular (18 K–L) ————]	
THICK TUBE										
Origin	[———— Dorso-lateral (17 A, D) ————]			[———— Sub-disto-dorsal (17 B, E) ————]		Disto-dorsal (17 C, F)	Ventral (18 A–C)	[———— Disto-ventral (18 D–E) ————]		Disto-dorsal (18 F)
Direction from origin	[———— **DORSO-LATERO-CEPHALAD** ————] (17 A, D)			[———— **DORSO-CEPHALAD** ————] (17 B–C, E–F)			[———— **VENTRO-CAUDAD** ————] (18 A–F)			
Length of proximal bends	[———— 3 times length of short bursa ————] (17 A, D)			[———— About 1/2 length of short bursa ————] (17 B–C, E–F)			1/3 length of elongate bursa (18 A–C)	[———— 2/3 length of elongate bursa ————] (18 D–F, J–L)		
Dilation of proximal bends	[———— Uniformly wide ————] (17 D)			[———— Uniformly narrow ————] (17 E–F)			Uniformly narrow or one small dilation (18 A–C)	[———— A large dilation in each bend ————] (18 D–F, J–L)		

TABLE 3
COLOR CHARACTERISTICS IN *BARYTETTIX* SPECIES

	poecilus*	crassus	terminalis	tridens*	h. humphreysii	h. cochisei	contilus	psolus*	nigrofasciatus	paloviridis
GROUND COLOR										
Gray	.	.	.	.	X	X	.	.	.	.
Brownish, or yellow brown	.	.	.	S	X	X	X	X	X	R[1]
Green, olive or yellow-green	X	X?	X	.	S	S	.	.	.	X
Blue, or yellow and blue	.	.	.	N						
PRONOTUM, LATERAL LOBES										
Dorso-longitudinal black bar										
Continuous and equal across lobes or inconspicuously narrowed caudad and cephalad	.	.	.	.	.	.	X	X	X	
Conspicuously weak, or narrow on metazona	.	.	.	.	.	.	X	X	NR	
Absent on metazona	X	X	X	X	X	X	.	.	.	X
Conspicuously broken on prozona	X	X	X	X	X	X	X	X	R	X
Ventral quarter										
Yellow	.	.	.	.	.	.	X	X	X	
Not yellow, but same as ground color	X	X	X	X	X	X	.	.	.	X
Ventral carina										
Black	.	.	.	.	.	.	X	X	X	R[2]
Not black, but same as ground color	X	X	X	X	X	X	.	.	.	X
HIND FEMUR, DORSAL STRIPE OF PAGINA										
Absent or inconspicuous	S	.	X	S?	S	R	.	.	.	X
Green, brown, blue, or weakly defined	X	X	.	X	X	X	.	.	S	X
Jet black and sharply defined	.	.	.	X	.	.	X	X	N	
HIND TIBIAL COLOR[3]										
Unicolored	X	X	X	X	N	N	X	X	S	X
Conspicuously bicolored	R	.	X	.	S	S	X	X	N	
Yellow	.	.	.	.	N	RN			.	.
Orange	.	.	.	.	N	RN		.	S	.
Red	S	X	.	.	X	N	X	.	.	
Wine	N	.	X	.	X	S	X	X	N	X
Purple	N	.	.	.	S	.	X	X	N	RS
Blue	S	.	.	X	.	.	X	N		
ABDOMEN, MEDIO-LONGITUDINAL YELLOW STRIPE										
Present, broad and usually black bordered	N	X	.	X	X	X	X	X	X	X
Absent, or present as a thin whitish line	S	R	X							.

X the commonest condition in many or all colonies of the species.
R rare, found as individual variants or in a few scattered colonies.
N the common condition found in northern colonies only.
S the common condition found in southern colonies only.

[1] only in some individuals near Guaymas and Altata.

[2] only in a few brown individuals, black on the ventral, but not on the outer surface.

[3] the geography of tibial color is often helpful in making probable identifications, see Tables 5 (*poecilus*), 10 — 11 (Psolus Group), 14 (*humphreysii*), 15 — 16 (*cochisei*). However, extension to areas, especially in the mountains, not treated in this paper is questionable. When using these tables for specimens found between Guaymas and Mazatlan the area of overlap of many species, it should be noted that *paloviridis* is wine legged, except for a few individuals with purple legs south of Culiacan, and that *poecilus* is always purple-legged in that region.

* see Frontispiece.

TABLE 4

DISTRIBUTION OF CHARACTERISTICS IN THE CRASSUS GROUP

(Bold-face type indicates easily recognizable, "key" characteristics.)

Character	*poecilus*	*crassus*	*terminalis*
Supra-anal plate: lateral processes (Figs. 8 A–B)	None or fine spines to wide-based teeth	Small spines or tubercles	Weak swellings to short, small teeth
Cercus: dorsal margin (Figs. 6 Q-X)	Barely concave	Weakly concave	Moderately concave
Cercus: disto-dorsal portion (Figs. 6 Q-X)	**Barely enlarged**	Weakly enlarged	Moderately enlarged
Dorsal valves: median notch (Figs. 7 B, D, F; 8 C)	**Moderately deep, V-shaped**	**Shallow, very broadly V-shaped**	**Moderately deep, narrowly V- or U-shaped**
Ventral aedeagal valves: lateral margins (Figs. 7 B, D, F; 8 D-E)	Smoothly convex or straight	Obtuse-angulate, distally almost straight	Obtuse-angulate, **distally concave**
Ventral aedeagal valves (Figs. 7 A, C, E-F)	Strongly down-curved	Strongly down-curved	**Strongly out-curved**
Ventral aedeagal valves: ventral ridge (Figs. 7 B, D, F; 8 D-E)	Oblique to almost longitudinal	Almost transverse	Oblique
Ramus of the cingulum: dorso-lateral surface (Figs. 7 A-F)	Smooth	Smooth	**With a large knob**
Ramus of the cingulum: ventro-medial margins (Figs. 7 B, D, F)	**Weakly divergent**	Moderately divergent	Strongly divergent
Hind femur: dorsal dark stripe on pagina (Frontispiece)	Present in north, absent in south	Present	Absent
Hind femur: carinae (Frontispiece)	Black or dark green	Gray-green	Usually green, if darker, then only distad
Dorsal abdominal yellow stripe (Frontispiece)	Often absent, usually inconspicuous when present	Apparently well-developed	Barely indicated
Hind tibia: color (Frontispiece)	Purple, reddish or blue	Red	Purplish-red

Color comparisons of all species of the genus may be found in Table 3, p. 25. Some specimens of *poecilus* are indistinguishable from some green *humphreysii* and *paloviridis* on the basis of color alone. However, green *humphreysii* occurs far to the north, and the red and purple-legged *paloviridis* are also allopatric to the *poecilus* which they resemble (see Table 5, p. 28, and the discussion of geographic variation under *paloviridis*, p. 53).

Within the Crassus Group, *poecilus* closely resembles *crassus* in most of the characteristics by which it differs from *terminalis*. These comparisons are summarized in Table 4, and their phylogenetic implications are discussed below in a section dealing with relationships among all *Barytettix* species.

SPECIES DESCRIPTION.— SUPRA-ANAL PLATE (Fig. 8 A): medio-lateral processes absent or varying from swellings through small, narrow spines to large, wide-based teeth. CERCUS (Figs. 6 S-X): weakly incurved; dorsal margin weakly concave; disto-dorsal portion slightly enlarged; disto-ventral tooth not at all, to moderately produced, rectangulate to acute. AEDEAGUS (Figs. 7 A-B): short (0.05-0.06 times length of pronotum), wider than long (length 0.76-0.92 times greatest width). DORSAL VALVES (Fig. 8 C): dorsally with a deep longitudinal furrow on either side of mid-line, medial portion strongly convex, lateral portions strongly bent upward, so that valves appear W-shaped in distal view; free lobes short, broad, apices blunt rectangulate, medial margins forming a moderately deep V; lateral margins straight or weakly concave in proximal half, then flaring and convex to apices, distal expanded portions if flattened would appear intermediate in length and width between *crassus* and *terminalis*. VENTRAL VALVES: in caudal view (Figs. 8 D-E), usually gently tapering from near base, lateral margins straight and parallel or convex; medial margins straight and weakly divergent or parallel; apices rounded, truncate or briefly blunt acute; ventral surface of each valve with a prominent, oblique, curved ridge which rounds into outer margin near middle, sometimes forming convex bulging portion of that margin; surface cupped between ridges, becoming flat distad; in lateral view (Fig. 7 A), evenly bent ventrad; in distal view, each valve with a longitudinal ridge on dorso-medial margin largely obscured by dorsal valves. RAMUS OF CINGULUM (Figs. 7 A-B): ventro-distal portion broad, strongly developed and projecting distad to level of junction of dorsal valves with ventral lobes of sheath, thus reducing ventral lobes to a narrow collar below ventral valves: dorso-laterally smooth, ventro-laterally rough and variably rugose; in caudal view (Fig. 7 B), ventro-lateral margins sub-parallel, medial margins weakly divergent. VENTRAL LOBES OF SHEATH (Figs. 7 A-B): forming a narrow collar below ventral valves; lateral portions usually extending distad of ramus and visible in side view; ventral portions with a brief flange curled dorsad toward ventral valves. BURSA COPULATRIX AND THICK TUBE (Figs. 17 A, D): very short and broad (width about twice the length), triangular, proximally with a moderately well-developed sclerite on each side, distally pleated, and strongly sclerotized at or possibly within orifice of thick tube; thick tube arising dorso-laterally and proceding dorso-cephalad, wide at origin and sclerotized there, moderately dilated immediately beyond origin, thence gradually narrowing, length between proximal bends moderate but much greater than bursa. COLORATION (Frontispiece): ground color green with a small amount of yellow. Head without yellow post-ocular stripes. Pronotum with dorso-lateral yellow stripes very narrow and not extending onto metazona, apparently often absent (possibly the result of poor preservation); black spot of lateral lobes not extending onto metazona, usually completely broken by cephalic diagonal yellow line, caudal horizontal line usually absent, when present weakly defined, spot narrowly bordered ventrad by yellow, ventral third of lobe and ventral carina green. Epimera partly black in north, green in south. Abdominal mid-dorsal yellow stripe often absent, especially in south, when present usually inconspicuous (possibly the result of poor preservation); tip of abdomen often weakly tinged with color of hind tibia. Hind femur with pagina in south unicolored green, in north with a dorsal green or brown stripe and a ventral yellow or yellowish-green stripe; carinae dark green or black; geniculae usually tinged with color of hind tibia and with black lunae. Hind tibia purple, reddish, or blue. MEASUREMENTS: those of the series studied are summarized in Figures 19 and 20.

GEOGRAPHIC VARIATION.— The geographic variation displayed by this species in four characters is summarized in Table 5. Only critical localities are listed. Others from which material has been examined have been indicated as lines connecting listed localities. Transitions between the variant characteristics are relatively abrupt geographically, with little intermediacy or mixture of characteristics (except in the transition between small and absent supra-anal plate processes). Exceptions are indicated in the table by parenthetical data, the fraction representing the proportion of that particular population showing the deviant character. The difference between the extreme conditions of the ventral valves is obvious (see Figs. 8 D and E), but individual variation and the technical difficulty of comparing specimens makes difficult the determination of the nature and position of the break. In this character, there may be a more gradual transition, and more mixture of characteristics in the El Venadillo-Villa Unión region than is indicated in the table. Southeast of the Villa Unión populations, there is little variation in the ventral valves.

The strong break in two and possibly three characters at the Río Presidio suggests that large rivers play a major barrier role in the dispersal of *Barytettix* species, as is also suggested in the variation in *paloviridis* and the distribution of *psolus*. In the region of the Río Presidio collections where vegetation, climate and other Orthoptera are relatively uniform, it is difficult to envision strongly different selective factors on either side of the river which would account for the difference observed. There is evidence that the three characters are independent of one another in the few individuals which show different combinations of these characters, and there is no evidence to indicate that the characters arose together. Thus, the break in all three

TABLE 5

GEOGRAPHIC VARIATION IN *BARYTETTIX POECILUS*

Localities (distances in miles)	Tibial Color	Paginal Stripe	Ventral Valve Ridge (Figs. 8 D-E)	Supra-anal Processes (Figs. 8 A-B)
66 SE Culiacán (70 N. Mazatlán)	PURPLE sometimes reddish distad or bluish proximad	DARK	LOW, STRONGLY CURVED	WIDE TEETH
El Venadillo (5 N Mazatlán)				
1.3-2.6 NW Villa Unión		DARK (1/11 light)*	LOW, STRONGLY CURVED	WIDE TEETH (1/6 small, thin)*
— — — — — — — — Río Presidio at Villa Unión — — — — — — — — —				
2 E -2.4 NE Villa Unión		LIGHT OR NONE (4/15 light)*	HIGH, WEAKLY CURVED	SMALL, THIN
15.1 SW Santa Lucía (NE Concordia)	(1/7 reddish)*			
26 NW Escuinapa		(1/5 light)*		
5 N Acaponeta	PURPLE			
1 W Acaponeta, 2 S Acaponeta	REDDISH			
— — — — — — — — Río Acaponeta — — — — — — — — —				
3 SE Acaponeta				SMALL; REDUCED; OR ABSENT
Tepic	(2/2 purple* 12 S. Jalisco)			
Plan de Barrancas (E Ixtlán del Río)	BLUE OR PURPLISH	LIGHT OR NONE	HIGH, WEAKLY CURVED	USUALLY ABSENT

*Fractions indicate proportion of population with indicated characteristic.

at the river probably means that there has been little communication across it in recent times. Each character has a wide distribution northwest or southeast, and must therefore have been in existence for a considerable period of time. That there is some crossing of the river is suggested by the presence of a very few individuals with some eastern characteristics (but not in combination) on the west side, and the possible influence of western paginal color on the east side populations. The continuity of the fourth character, tibial color, across the river is probably to be explained by the possession of this color by the ancestral populations which either crossed the river, or whose distribution was split by it. Farther south tibial color shifts from purple to red on the west side of the Río Acaponeta and within seven miles of that river. Either the red characteristics has just crossed the river northwestward, or the red of these populations has not yet been replaced by purple moving southeastward. The blue-legged populations near Ixtlán del Río represent a geographically isolated sample, but is probably connected to the coastal plain populations by colonies in the valley of the Río Grande de Santiago where we have not collected.

Larger samples near both the Río Presidio and the Río Acaponeta, and samples farther upstream might provide more definitive evidence on the problem. It might also be instructive to continue to sample these populations over a period of years and thus possibly determine the rate of movement of the characteristics.

HABITAT AND ASSOCIATED SPECIES.— This is a common species in weedy, bushy habitats along the road in thorn forest and tropical deciduous forest zones. It has been found within thorn forest at several localities, in thin weedy and bushy vegetation. It has also been found in open oak woodland at 2950 feet in Nayarit, in rather thin weedy, grassy vegetation with scattered bushes. However, farther north on the Mazatlán-Durango Highway, *poecilus* apparently does not extend into the oak zone, which begins at about 3500 ft., although the lower edge of this zone has been sampled at only a few localities.

The northernmost colonies of *poecilus* are sympatric with the southernmost colonies of *tridens, paloviridis* and the three known colonies of *contilus similis*. Between 66 and 77 mi S of Culiacán, various combinations of *poecilus* and two of the other species occur (see Table 19).

Poecilus is also sympatric with *nigrofasciatus* at most of the known localities for the latter between Santa Lucía and Concordia and at San Ignacio.

The distributional pattern of *poecilus, paloviridis,* and *psolus* in the region of the northern limits of *poecilus* invites some interesting questions concerning the factors limiting the distribution of that species. Because of the rarity of *tridens* in this region, it is ignored in the following discussion. Along the west coast highway, *poecilus* and *paloviridis* overlap for about 10 miles. Immediately north of this zone we have many collections of *paloviridis* at short intervals but neither *poecilus* nor *psolus*. East of this zone, we have collections from two roads. That leading to Cosalá leaves the west coast highway in the middle of the overlap zone. Fourteen miles northeast of this junction, and about 600 feet higher, our first collection contains only *paloviridis* and *psolus,* both of which were common. At several localities in the vicinity of Cosalá, 14-25 miles beyond the first and at about 1500 feet, only *psolus* was found in abundance. The habitat at the first locality was rich thorn forest or transitional to tropical dediduous forest, and that at the Cosalá localities was transitional or rich tropical deciduous forest. On this road we have another set of collections west of the *poecilus-paloviridis* coast highway overlap zone on the road leading to San Ignacio. Along this road, which leaves the coast highway fourteen miles south of the overlap zone, the two species are geographically sympatric but occur in apparently slightly different habitats. Thus, *paloviridis* was found to be common, and *poecilus* absent at 4.6 mi E Coyotitán, whereas *poecilus* occurred within a mile to the east in a slightly bushier habitat. At 1.1 mi SW San Ignacio Ferry, *paloviridis* was found only in the weedier parts of a cut-over roadside area, whereas *poecilus* occurred generally in more bushy areas as well as in the weedy patches. In view of the abundance of *paloviridis* in many habitats north of the overlap zone, the similar abundance of *poecilus* south of the zone, and the occurrence of *poecilus* up to 3500 feet about 50 miles to the south on the Mazatlán-Durango Highway, the restriction of *poecilus* northward and upward in the overlap zone may thus be the result of interaction with its congeners. This area is relatively little disturbed by man and *poecilus* is generally common here. It would be an ideal area to study

the possibility of competitive exclusion in these herbivorous species.

SEASONAL OCCURRENCE.— Earliest records for adults of this species are 26 and 27 July at 4.3 and 11.5 mi NE Concordia. Many of these individuals were teneral, and late instar nymphs were abundant. Our latest record is 28 November at 1.1 mi SW San Ignacio Ferry. The species was common then, suggesting a longer life, but no nymphs were seen. Cantrall failed to find any *Barytettix* in early April when he spent two weeks collecting for Orthoptera at several lowland localities between San Blas and Mazatlán. The above evidence suggests that the eggs hatch in the summer, perhaps by the first summer rains as we have suggested for *paloviridis* on the basis of other evidence, and that the adults die in early or mid-winter.

DISTRIBUTION.— The northwesternmost record for *poecilus* is 66 mi SE Culiacán, Sinaloa, the southeasternmost, 5.4 mi E bridge at Plan de Barrancas, Jalisco.

RECORDS.— Specimens examined: 232 ♂♂, 166 ♀♀, and many juveniles reared to maturity. Other than material listed in Table 19, we have examined specimens from the following localities, all in México: NAYARIT: 5 mi N Acaponeta on Huajicori Mine Road (1), 1 mi W Acaponeta (1), 2 mi S Acaponeta, at Hwy. No. 15 river bridge (4), 3.1 mi SE Acaponeta (4), 4.9 mi SE Acaponeta on Hwy. No. 15 (2), 8.6 mi SE Acaponeta (7), 9.6 mi SSE Acaponeta (6), 25 mi SE Acaponeta on Hwy. No. 15 (6), 31 rd. mi NE Tepic on Hwy. No. 15 (5), 2.2 mi NE Río Santiago (6), 17.9 mi NW Tepic on Hwy. No. 15 (7), 15 mi N Tepic (AMNH) (2), 14.4 mi NW Tepic (14), 12.7 rd. mi S Jalisco on Compostela Road (2), 4 mi N Compostela (3); JALISCO: 20 mi N La Quemada (AMNH) (1), 5.4 mi E bridge at Plan de Barrancas (6).

Barytettix crassus Scudder
Figs. 6 R, 7 C-D

Barytettix crassus Scudder, 1897, Proc. U. S. Nat. Mus. 20:27-28, Pl. II, Fig. 10. [Holotype, ♂, San José del Cabo, Lower California. [Territorio de Baja California]; Hebard Collection in the Academy of Natural Sciences of Philadelphia.]

DIAGNOSIS.— Males of this form may be distinguished from all other species of *Barytettix* by the briefly and broadly notched dorsal aedeagal valves (Fig. 7 D) or by the strongly and broadly produced disto-ventral tooth and the weakly enlarged disto-dorsal portion of the cercus (Fig. 6 R). In other species the cercus sometimes approaches the condition found in *crassus*, but the cercus is either strongly incurved and twisted with the disto-dorsal portion distinctly expanded, or the insect has a brown ground color, or an elongate aedeagus indicated in undissected speci-

mens by an enlarged pallium. Female *crassus* can be distinguished only by a combination of color and receptaculum seminis characteristics. The species is apparently always green, and may be distinguished from *paloviridis* and green *humphreysii* by the short bursa copulatrix and broad dorso-lateral thick tube. From *terminalis* it may be distinguished by the dark carinae and paginal stripe of the hind femora and by the mid-dorsal abdominal yellow stripe, and from *poecilus* by the combination of those two characteristics and the red hind tibiae (Table 4, p. 26). The uniformity of the color characteristics for *crassus* is as yet unknown because of poor preservation and the small number of localities from which we have material. Our preliminary measurements based on larger series do not bear out Gurney's (1951) suggestion that the hind femora of *crassus* are more robust than those of *poecilus*.

Color comparisons of all *Barytettix* species may be found in Table 3, p. 25, and the geography of the color characteristics in *poecilus* may be found in Table 5, p. 28. *Crassus* probably cannot be recognized by color alone from most *paloviridis* or from some *humphreysii*.

Within the Crassus Group, this species is similar to *poecilus* in most of the characters by which it differs from *terminalis*. These comparisons are summarized in Table 4, p. 26, and the phylogenetic implications are discussed below in a section dealing with the relationships of all species of *Barytettix*.

SPECIES DESCRIPTION.— SUPRA-ANAL PLATE: medio-lateral processes either small spines or tubercles. CERCUS (Fig. 6 R): weakly incurved; dorsal margin weakly concave; disto-dorsal portion weakly enlarged; disto-ventral tooth strongly and broadly produced, acute. AEDEAGUS (Figs. 7 C-D): short (0.05-0.08 times length of pronotum), wider than long (length 0.67-1.0 times greatest width). DORSAL VALVES (Fig. 7 D): dorsally with a deep longitudinal furrow on either side of midline, medial portion strongly convex, lateral portions strongly bent upward, so that valves appear W-shaped in distal view; free lobes short, moderately broad, apices truncate, blunt rectangulate or rounded, medial margins forming a brief narrow medial U, then flaring to form a wide V, the entire medial excision shallow, lateral margins barely flaring in dried material, if flattened, distal expanded portion would appear narrower and shorter (more distad) than in *poecilus* and *terminalis*. VENTRAL VALVES: in caudal view (Fig. 7 D), strongly tapering; lateral margins obtuse-angulate in proximal quarter, thence converging but slightly concave to near apices where margins converge sharply to short, medially directed angulate apices; ventral surface of each valve with a strong, almost transverse ridge in proximal quarter which forms the obtuse angle of lateral margins, surface distad of ridge slightly cupped; in lateral view (Fig. 7 C), gently curved ventrad; in distal view, each valve with a longitudinal ridge on dorso-medial margin largely obscured by dorsal valves. RAMUS OF CINGULUM (Figs. 7 C-D): ventro-distal portion broad, strongly developed and projecting distad to level of junction of dorsal

valves with ventral lobes of sheath, thus reducing ventral lobes to a narrow collar below ventral valves; dorso-laterally smooth, ventro-laterally with a few strong tubercles or rugose; in caudal view (Fig. 7 D), ventro-lateral margins sub-parallel, medial margins moderately divergent. VENTRAL LOBES OF SHEATH (Figs. 7 C-D): forming a narrow collar beneath ventral valves, lateral portion extending distad of ramus and visible in side view, ventral portion in distal view with a brief flange curled dorsad toward ventral valves. BURSA COPULATRIX AND THICK TUBE (similar to Figs. 17 A, D): short and broad (width about twice the length), triangular, moderately pleated, proximally weakly sclerotized laterad, region of orifice of thick tube weakly sclerotized; thick tube arising dorso-laterally and proceeding dorso-cephalad, wide at origin and moderately dilated immediately beyond origin, thence gradually narrowing, length between proximal bends moderate but much greater than bursa. COLORATION (based on dried alcoholics from San José del Cabo, and discolored specimens from San Bartolo and Puerta Azul Mesa): ground color possibly greenish or olive green (best preserved specimens show a tinge of green, others are brown), probably with a small amount of yellow. Head apparently with narrow post-ocular yellow stripes. Pronotum apparently with dorso-lateral yellow stripes narrow, not extending onto metazona; black spot on lateral lobes usually restricted to pro- and mesozona, rarely extending briefly onto metazona, sometimes extending to caudal margin as a weak wash, spot usually entire, rarely weakly cut by narrow, irregular cephalic diagonal light line, that line usually well-developed only ventrad, making black spot appear narrow cephalad, caudal horizontal yellow line usually absent, rarely barely and irregularly indicated by spots; black spot bordered ventrad by yellow, ventral quarter of lobe and ventral carina concolorous with metazona, probably greenish. Epimera almost entirely black. Abdomen apparently with mid-dorsal stripe well-developed, but poorly preserved in most specimens; black dorso-lateral markings well-developed, yellow dorso-lateral markings barely indicated, but probably poorly preserved; supra-anal and subgenital plates tinged with reddish. Hind femur with ventral half of pagina yellow, dorsal half greenish or brownish; carinae darker gray-green; geniculae tinged with reddish, with brownish or reddish lunae. Hind tibia unicolored red, apparently often fading to pinkish. MEASUREMENTS (in mm): those of the series studies are summarized in Figures 19 and 20.

HABITAT, ASSOCIATED SPECIES, AND SEASONAL OCCURRENCE.– We have no direct information about this species other than the locality and date on the pin labels from two small collections and a questionable third. The description and pictures of the vegetation at San José del Cabo and other lowland localities south of La Paz in Nelson (1921) suggest thorn forest, much like that around Mazatlán. Nelson indicates that Tropical Arid vegetation occupies the lowlands in this region and suggests that the tropical elements originated on the coastal plains and foothill slopes on the mainland directly opposite. We suspect that the collections were made in the lowlands because it seems likely that the extra effort of getting into the mountains would have been noted on the label. No other species of *Barytettix* are known from Baja California, but little collecting has been done there. The dates of collection range from 1 to 12 November at San Bartolo and Puerta Azul Mesa.

DISTRIBUTION.– *Crassus* is known from the tip of Baja California (female allotype of *Melanoplus nitidus* Scudder tentatively identified as *Barytettix crassus*) northward to San Bartolo (about 40 mi S La Paz). We have been unable to locate Puerta Azul Mesa, but suspect that it is close to San Bartolo from which specimens are labelled as having been taken the day after the Puerta Azul Mesa collection.

RECORDS.– Specimens examined: 9 ♂♂, 12 ♀♀ 3 juveniles. TERR. BAJA CALIF.: San José del Cabo (15) (UMMZ, ANSP[6]), San Bartolo (7) (USNM), Puerta Azul Mesa (2) (or Mesa Pta. Azul) (USNM).

Barytettix terminalis [7] n. sp.
Figs. 6 Q; 7 E-F

HOLOTYPE.– ♂, México, Jalisco, 16.2 mi NE Barra de Navidad (on Hwy. 80), 2 September 1968 (T. J. Cohn No. 33); University of Michigan Museum of Zoology.

DIAGNOSIS.– *Terminalis* may be distinguished from all other species of the genus by the strongly but briefly out-curved ventral aedeagal valves (Fig. 7 F), the dorso-lateral knob on the ramus of the cingulum (Fig. 7 F), and the concolorous or narrowly and inconspicuously blackened hind femoral carinae. Additional differences between *terminalis* and its relatives may be found in Table 4, p. 26, and the color comparisons with all *Barytettix* species are summarized in Table 3, p. 25.

Within the Crassus Group, *terminalis* stands apart from the other two members in the above three characteristics. In other characters it is about as similar to *poecilus* as it is to *crassus*. These comparisons are summarized in Table 4, p. 26, and their phylogenetic implications are discussed below in the section on the relationships of all *Barytettix* species.

SPECIES DESCRIPTION (in variable characters, condition in holotype indicated by asterisk preceding that condition).– SUPRA-ANAL PLATE: medio-lateral processes varying from

[6]All the material of this species at the Academy of Natural Sciences of Philadelphia except the type (3♂♂, 6♀♀, 3 juvs.), as well as a pair from the University of Minnesota, now in the University of Michigan Museum of Zoology, bear locality labels similar in size, paper, type and arrangement of words, but which differ slightly in spelling and punctuation. Only the type label bears the collector's name, G. Eisen. All have been dried from liquid and have the same appearance. They are all probably part of the original series of which Scudder apparently saw only the one male which he described.

[7]In reference to the southernmost position of this species in the distribution of the genus and to the fact that it was discovered in the terminal stages of this study.

swellings to *short, small teeth. CERCUS (Fig. 6 Q): moder-
ately incurved and sometimes slightly twisted; dorsal margin
moderately concave; disto-dorsal portion moderately enlarged
and elongated; disto-ventral tooth *weakly to moderately pro-
duced, acute. AEDEAGUS (Figs. 7 E-F): short (0.07-0.08 times
length of pronotum), wider than long (length 0.75-0.90 times
greatest width). DORSAL VALVES (Fig. 7 F): dorsally with a
deep longitudinal fold or furrow on either side of mid-line,
medial portion strongly convex, lateral portions strongly bent
upward, so that valves appear W-shaped in distal view; free lobes
very short, broad, apices more or less truncate, medial margins
forming a moderately deep, very narrow *V or U, lateral margins
diverging from near base, weakly angulate near middle, thence
rounding to medial margins, distal expanded portion if flattened
would appear generally longer and wider than in *crassus* and
poecilus. VENTRAL VALVES: in caudal view (Fig. 7 F), lateral
margins strongly rectangulate in proximal quarter, thence strong-
ly concave to short, outward-twisted, blunt acute apices; ventral
surface of each valve with a strong oblique ridge on proximal
quarter which becomes almost flange-like laterad and forms the
angle on lateral margin of valve; surface between and distad of
ridge tilted dorsad laterally to near apex where it becomes more
or less flat; in lateral view (Fig. 7 E) more or less straight; in dis-
tal view, each valve with a longitudinal ridge on dorso-medial
margin largely obscured by dorsal valves. RAMUS OF CINGU-
LUM (Figs. 7 E-F): ventro-distal portion broad, strongly devel-
oped, and projecting distad to level of junction of dorsal valves
with ventral lobes of sheath, thus reducing ventral lobes to a
narrow collar below ventral valves; dorso-lateral portion with a
prominent knob, ventro-lateral portion rugose, in caudal view
(Fig. 7 F), ventro-lateral and medial margins strongly divergent.
VENTRAL LOBES OF SHEATH (Figs. 7 E-F): forming a
narrow collar beneath ventral valves, lateral portion usually *not
extending distad of ramus and thus usually invisible in side view.
BURSA COPULATRIX AND THICK TUBE (similar to Figs.
17 A, D): short and broad (width 1.3 to about 2 times length),
triangular, proximally with a well-developed sclerite on either
side, distally moderately pleated, region of orifice of thick tube
strongly sclerotized; thick tube arising dorso-laterally and pro-
ceeding dorso-cephalad, wide at origin and moderately dilated
immediately beyond origin, thence gradually narrowing, length
between proximal bends moderate but much greater than bursa.
COLORATION: ground color green with almost no yellow.
Head with narrow post-ocular stripes. Pronotum with dorso-
lateral yellow stripes narrow, not extending onto metazona;
black spot of lateral lobes not extending onto metazona, com-
pletely broken by cephalic diagonal yellow line which is narrow,
caudal horizontal line barely indicated and broken in females,
absent in males, spot narrowly bordered ventrad by yellow,
ventral third of lobe and ventral carina green. Epimera varying
from entirely green, through *green margined with black, to
largely black. Mid-dorsal abdominal stripe *barely indicated,
narrow and not margined in a few specimens; dorso-lateral
yellow markings narrow and inconspicuous, absent in several
specimens; dorso-lateral dark margins narrow; tip of abdomen
tinged with reddish. Hind femur with pagina unicolored green,
carinae usually green, sometimes *narrowly and inconspicuously
black, geniculae tinged with color of hind tibia and with black
lunae. Hind tibia purplish-red (more purple than southern popu-
lations of *poecilus*). MEASUREMENTS (in mm): holotype
male: length of body, 25.61; length of pronotum, 4.69; length
of tegmen, 3.77; length of fore femur, 4.73; length of hind
femur, 13.53; greatest width of hind femur, 3.75. Measurements
of the series studied are summarized in Figures 19 and 20.

PARATYPES.— Other than the holotype, all
adult specimens examined in this study are desig-
nated as paratypes. Male and female paratypes
are deposited in the University of Michigan
Museum of Zoology, the Academy of Natural

Sciences of Philadelphia, the United States Na-
tional Museum, and the Instituto de Biología,
Universidad Nacional de México.

HABITAT, ASSOCIATED SPECIES, SEASONAL OC-
CURRENCE, AND DISTRIBUTION.— This species
is known from only two localities a few miles
apart in the coastal range of low mountains in
southwestern Jalisco. The vegetation in this
region is characterized as Tropical Subdeciduous
Forest by Rzedowski and McVaugh (1966). The
specimens collected at the type locality were
found at the mouth of a canyon with tall trees,
many vines and heavy undergrowth. They were
most common in the narrow roadside strip of
lush but low weeds and bushes and some were
found in the edge of the forest. At the second
locality, 2.1 miles farther inland, the forest was
lower, but collections were made in the more
open cleared roadside areas with scattered spiny
bushes and variably dense weeds. A number of
other localities have been investigated in Colima
and western Jalisco and southwestern Nayarit at
high as well as low elevations. Neither *terminalis*
nor any other species of *Barytettix* has been
found, although *poecilus* has been found at
higher elevations near Compostela and Tepic,
Nayarit, and is common north of Tepic on the
coastal plain. At the type locality, 16.2 mi N
Barra de Navidad, *terminalis* was found with a
similarly large species of a related new genus.
The earliest record for this species was 31 August
and the latest 6 October. On the latter date only
one male was found and females were not com-
mon, although other orthopterans were abundant.

RECORDS.— Specimens examined: 9 ♂ ♂, 18 ♀ ♀, and
several juveniles reared to maturity. JALISCO: 18.3 mi N Barra
de Navidad (on Hwy 80) (12); 16.2 mi N Barra de Navidad (on
Hwy 80) (15).

THE PSOLUS GROUP

Most of the *Barytettix* populations in the mid-
dle portions of the range of the genus possess a
highly distinctive, elongate aedeagus and recepta-
culum seminis, and share several distinctive de-
tails of these structures. We have grouped these
populations together as a species group, consist-
ing of four new taxa, *paloviridis, psolus, con-
tilus* and *nigrofasciatus*. Our reasons for dividing
the group into four species are discussed in detail
below.

The distinctive features shared by all four
forms of the group follow:

AEDEAGUS (Figs. 1 C-D)
1. Shape elongate (at least 0.19 times length of pronotum), projecting dorsally from genital cavity into a sac-like enlargement of the pallium (Fig. 15 H), narrow (length at least 1.6 times width, compared to sub-quadrate in other species groups).
2. Ventral valves more or less straight in lateral and caudal views, strap-shaped in caudal view, lateral margins subparallel (sometimes slightly broader across middle), apices in caudal view acute or rounded acute (never aciculate or down- or out-curved).
3. Ramus of cingulum with ventro-distal portion narrow, and ending considerably proximad of junction of dorsal valves with ventral lobes of sheath, thus exposing a lengthy portion of ventral lobes (as in Humphreysii Group).
4. Ventral lobes of sheath elongated distad of junction with dorsal valves as a pair of parallel, approximate, finger-like projections, these often projecting along their entire length at an angle from ventral valves, thus giving the aedeagus a fork-shaped appearance in lateral view; apices in distal view irregularly oval, the two parallel or forming an acute angle (flattened and forming an obtuse angle only in *paloviridis* from Guamúchil).
5. Proximal portion of ventral lobes of sheath usually keel-shaped, and always provided with an elongate sclerite on either side (the process of the ramus of the cingulum) which is readily visible in dried preparations.

BURSA COPULATRIX (Figs. 16 C, 18)
Elongate and narrow (length at least 1.9 times width, compared to length equal to or shorter than width in other species groups), strongly sclerotized; in cross-section concave dorsally, convex ventrally; sclerotization divided into proximal and distal sclerites by a colorless flexible area, proximal sclerite strongly pleated dorso-laterally and appearing weak or colorless along mid-line.

THICK TUBE (Figs. 16 C, 18)
Originating distally or ventrally, and proceeding immediately caudo-ventrad, proximal bends usually half the length of bursa, and each bend usually provided with a bladder-like dilation (in *contilus*, proximal bends about one-fourth the length of bursa and usually without dilations).

The following distinctive color pattern is found in the three brown species of the group (*psolus, contilus* and *nigrofasciatus*) (Frontispiece):

1. Pronotum with dorso-lateral yellow stripes usually reaching caudal margin.
2. Lateral lobes of pronotum with dorso-longitudinal dark band extending to caudal margin, often lighter and narrower on metazona.
3. Ventral third of lateral lobes yellow, with black ventral carina.
4. Pagina with sharply defined, jet black stripe on dorsal half (often lighter and poorly defined in *nigrofasciatus*).

In the field, males of this group may be readily identified by the sac-like enlargement of the pallium (Fig. 15 H), and by the forked appearance of the extruded aedeagus as seen from the side (Figs. 13 A, C, E). Females of *psolus, contilus* and *nigrofasciatus* may be distinguished by the color pattern described above. *Paloviridis* is similar in color and pattern to the Crassus Group and to the green populations of *humphreysii* (see Table 3, p. 25, for a comparison of the color and color pattern of all species of the genus).

The systematic status of *Barytettix* populations with these characteristics poses theoretical and practical problems, and the solutions which we offer here require comment on our methodology. These populations fall into two color types (Table 6), both of which have the black and yellow spots and maculations found in all species of the genus. In one type, the ground color of the body is green, and in color and pattern this type is identical to the green color types found in the Humphreysii and Crassus Groups. In the other type, the ground color is yellow-brown with special black and yellow markings (listed above) not found in other species of the genus. These two color types overlap broadly in Sinaloa, and individuals of both are commonly found in the same habitat if not in the same bush. Although there is considerable genitalic variation within each color type, in the many localities where the two are sympatric, all individuals possessing any one genitalic type (each type always differing in several characters from any other) are invariably of the same color type. Nor does the green type ever have any of the special markings of the brown type within this area of sympatry. It is therefore evident that in each locality the two color types are reproductively isolated and are acting as good species. We

TABLE 6

DISTRIBUTION OF CHARACTERISTICS IN THE PSOLUS GROUP

(Bold-face type indicates easily recognizable, "key" characteristics)

Character	contilus	psolus	nigrofasciatus	rubramdis
COLOR (Frontispiece)				
GROUND COLOR (exclusive of black and yellow markings)		Brownish		Usually **green** (brown only near Guaymas and Altata)
LATERAL LOBES OF PRONOTUM				
Dark stripe on metazona		Present, but sometimes very narrow and light		Usually absent (present but very light only near Guaymas)
Ventral third		**Yellow**		Usually **green** (**brown** when ground color brown)
Ventral carina		**Completely black**		**Green** (**brown** when ground color brown, rarely black on ventral surface only)
PAGINAL DARK STRIPE		**Black and sharply defined**	Or brown or gray and weakly defined	Absent, dark green or brownish
HIND TIBIA	Unicolored or bicolored; red, purple or blue, or combinations	Unicolored blue or red; or bicolored blue-purple to blue-red	Unicolored red or purplish; or bicolored blue-purple or blue-wine	Unicolored red-wine or purplish
AEDEAGUS				
DORSAL VALVES (Fig. 14)				
Position of apices		**Lateral** or latero-dorsal (but with dorsal projections in *contilus*)		Dorsal, and **near medial margin** of each ventral valve
Hump on fused portion (Figs. 13 and 15)	Usually absent (present in *c. tectatus*)		Present	Present in northern and southern populations
Inner margins	Parallel proximad, then diverging or with a **lobe** or **tooth**	Parallel proximad, divergent distad, never toothed	Evenly diverging from base, never toothed	Almost parallel, never toothed
Attitude	Flaring or appressed to ventral valves	Appearing to be **impressed into ventral valves**	Appressed to ventral valves or flaring distad	Flaring distad

VENTRAL VALVES (Fig. 14)				
Length of valve / length of pronotum	0.19 – 0.23	0.23 0.26	0.30	0.19 – 0.38 (0.19 – 0.23 values only north of 30 mi NW Culiacan)
Lateral walls of phallotreme (dorsal view)	**Broadly visible**	Narrowly visible distad	Narrowly visible	Invisible or narrowly visible distad
Lateral margins	Broadly convex (in *c. tectatus*, broad emargination extending proximad of middle)	Distinctly but briefly emarginate in distal half (at apices of dorsal valves)	Evenly and broadly convex	Evenly and broadly convex or weakly emarginate near or proximad of middle
Ventral surface	Variable, usually lengthily concave	With a medio-distal concavity	Flat	Flat, or swollen laterad near middle, or sometimes with medio-distal concavity
VENTRAL LOBE OF SHEATH				
Shape of dorsal margin in side view (Figs. 13 and 15)	Convex or appearing bent ventrad	Usually slightly convex, rarely straight	Almost straight to slightly convex	Usually straight, rarely weakly convex
Shape of apices in distal view (fig. 15)	Briefly thin, meeting at an angle		Oval to briefly thin and usually meeting at an angle	Round to **strongly compressed,** usually parallel (meeting at an angle only near Guamúchil) often **appressed**
RECEPTACULUM SEMINIS (Fig. 18)				
BURSA COPULATRIX				
Distal sclerotization	Distal or subdistal and continuous (or proximal and divided in *c. tectatus*)	Proximal and divided	Proximal and continuous	Medial and continuous
THICK TUBE				
Shape	**Gradually narrowing from origin** (or with one small dilation in *c. tectatus*)		With two **large bladder-like dilations**	
Location of orifice	Ventral	Disto-ventral		Disto-dorsal

have found four genitalic characteristics which correlate with the two color types: the position of the dorsal aedeagal valve apices, the shape of the ventral lobes of the aedeagal sheath in side view, the shape of the ventral lobes in distal view, and the position of the orifice of the thick tube of the receptaculum seminis (Table 6). Thus the color types appear to represent two separate lines of evolution.

Within the green color type we find complex geographic variation in many different characters and with much discordance. Part of this pattern of variation may be ascribed to reproductive interaction (but not interbreeding) with a closely related species, and the pattern suggests reproductive continuity throughout and beyond the region of sympatry. Designation of subspecies would serve no particular purpose and would obscure this situation as well as several puzzling discordant characters. The populations near Guamúchil display a few distinctive aedeagal characters, one of which is not uniform in its occurrence there. Again subspecific designation appears to be of no particular value. The northernmost green populations differ in several characters from the rest of the species, but are geographically widely separated from the nearest green populations to the south. We therefore cannot determine their status. They may merely represent the end of several clines. Finally, a few characters are largely discordant with others in the range of the species and the pattern can only be described. Thus it appears to be reasonable to describe the green color type as a single species (*paloviridis*) and to discuss each character and population variant separately.

The brown color type also displays considerable geographic variation but of a different kind. Genitalic differences are strongly concordant and sharply circumscribed geographically, but within any one genitalic type there is usually much geographic variation in tibial color. Two levels of similarity can be discerned. The northern and southernmost populations, although differing from each other in several details of genitalic structure, both differ from the middle populations in having a long aedeagus with the phallotreme walls invisible or only narrowly visible from above, a longer bursa copulatrix, and long dilated proximal bends of the thick tube (Table 6). The middle populations all share a shorter aedeagus with phallotreme walls broadly visible from above, a shorter bursa, and short, undilated bends of the thick tube, but they differ among themselves in genitalic details (Table 6). Each of the genitalic types of these middle short aedeagus populations is circumscribed geographically and, with one exception, each is morphologically quite uniform within its area. Only one genitalic type (*tectatus*) shows some similarity to the northern and southern long aedeagus populations, but is separated at least from its southern relative by three different middle aedeagal types. Despite variation of tibial color in some of these middle populations, it seems useful to designate each as a subspecies of a short aedeagus species (*contilus*) to emphasize their similarities. To the north as well as to the south, this species approaches the long aedeagus populations within a few miles. We have no evidence of introgression in these areas, and conclude therefore that the short aedeagus type is probably reproductively isolated from the two long aedeagus types. Despite their overall similarities, each of the latter is uniform in its genitalic differences from the other, as well as from the short aedeagus type. We are therefore designating the northern and southern long aedeagus types as two species, respectively *psolus* and *nigrofasciatus*.

The relationship between *psolus* and *nigrofasciatus* poses special problems. A gap of 35 miles separates their presently known ranges. Their genitalic differences appear to offer no barrier to the insemination of the females of either species by males of the other species (see discussion in the sections, Mechanical Isolation, and Promising Problems). On the other hand, there is no genitalic evidence from the geographically closest collections of the two forms that they ever have been in contact, although certain color characters are more similar there. The differences between them are sufficiently great and uniform to suggest that postzygotic incompatibilities already present might form the basis for the rapid attainment of complete reproductive isolation should the two forms meet. This may already have happened in the zone where no collections have yet been made.

The four species of the Psolus Group are compared and contrasted in Table 6. The characteristics in bold face type are the most distinctive and most easily used and thus may serve as key characters.

Barytettix contilus[8] n. sp.
Figs. 6 FF-JJ; 13 E-F; 14 A-E, I-M, Q-U;
15 I-J; 18 A-C, G-I

HOLOTYPE.— ♂, México, Sinaloa, 3 mi NE Tepuche (13.5 mi N Culiacán), 6 September 1966 (T. J. Cohn No. 40); University of Michigan Museum of Zoology.

DIAGNOSIS.— Males of this species may be distinguished from all other *Barytettix* species by the combination of a relatively elongate aedeagus, strap-shaped ventral valves without prominent shoulders (Figs. 14 I-M), and a phallotreme broadly but briefly exposed distally as seen from above (in contrast to the condition in *cochisei* in which the phallotreme is lengthily exposed by the widely separated dorsal valves, compare Figs. 14 A-E and 8 F). The elongate aedeagus is indicated in undissected specimens by a sac-like enlargement of the pallium, as in all members of the Psolus Group (similar to Fig. 15 H). Females of *contilus* may be distinguished from all others by the combination of an elongate bursa copulatrix and by small, undilated proximal bends of the thick tube (one small dilation in *c. tectatus*) (Figs. 18 A-C, G-I). Also distinctive in the bursa is the strong distal pleating and the distal position of the distal sclerite close to the orifice of the thick tube (neither condition holds for *c. tectatus*, but that subspecies is unique in the genus in having a subdistal ventral origin of the thick tube). Further comparison is made in Table 6, p. 34 . Color comparison of all species of the genus may be found in Table 3, p. 25 . *Contilus* may be distinguished by color from *psolus* and *nigrofasciatus* only by the geography of various of the color features. This is discussed under geographic variation of *psolus*. Tibial color comparisons are made in Table 11, p. 49 , under that species.

Within the Psolus Group, *contilus, psolus* and *nigrofasciatus* form a distinctive subgroup in femoral, pronotal and ground color characteristics, in the shape of the ventral lobes of the aedeagal sheath in side view, the position of the dorsal aedeagal valves, and the ventral or ventro-distal origin of the thick tube of the receptaculum seminis (Table 6, p. 34). The apices of the ventral lobes of the sheath in distal view are almost identical to those in *nigrofasciatus* and to individual variants in *psolus*. Of all the subspecies of *contilus, tectatus* shows the greatest similarities to other species of the group. The dorsal valves of this subspecies are similar to those in *nigrofasciatus* in their median hump, flaring lateral portions, and the general shape of their inner margins. *Tectatus* displays more detailed similarities to *psolus*, as summarized in Table 7. *Contilus* shares no distinctive characteristics with *paloviridis*, the fourth member of the Psolus Group. Comparisons of these features are summarized in Table 6 and their phylogenetic implications are discussed in the section on the relationships of all *Barytettix* species.

SPECIES DESCRIPTION (in variable characters, condition in holotype indicated by asterisk preceding that condition).— CERCUS (Figs. 6 FF-JJ): dorsal margin almost straight to *moderately concave; disto-dorsal portion not at all, to *moderately enlarged; disto-ventral tooth moderately produced, acute. AEDEAGUS (Figs. 13 E-F, 14 A-E, I-M, Q-U): moderately elongate (0.19-0.22 times length of pronotum, 0.21 in holotype), and narrow (length 1.6-1.9 times mid-dorsal width, 1.8 in type). DORSAL VALVES: in cephalic view (Figs. 14 A-E), *rounded from side to side, or roof-like, or flaring laterally; free lobes with median margins *parallel or weakly diverging proximad, thus forming a narrow V or *U there, then either diverging smoothly to latero-ventral acute apices, or each lobe with a dorso-medial *angle, lobe, tooth or prong, in addition to ventro-lateral acute apical angulation; fused portion sometimes with a broad, low, median hump, or *with low humps on free lobes; lateral margins variable, *convex, sinuate or straight; in lateral view (Fig. 13 E), ventro-lateral margin variable, straight, *sinuate or convex, concealing or *exposing ventral valve. VENTRAL VALVES: in cephalic view (Figs. 14 A-E), phallotreme widely open dorsally beyond dorsal valves, lateral walls visible from above and forming dorsally a strong *median or lateral ridge on each valve; in lateral view (Fig. 13 E), straight or *with apices curving weakly dorsad, valves thick *at or immediately proximad of apices of dorsal valves, the valves then immediately becoming thin, or *narrowing less rapidly to acute apices but appearing blunter; ventro-lateral margin obscured or *exposed by dorsal valves; in caudal view (Figs. 14 I-M), medial margins *separate from near base or only in distal third, lateral margins variously straight, concave, or *convex, ventral surface variously concave, *flat, or keeled. RAMUS OF CINGULUM (similar to Figs. 1 C-D): ventro-distal portion narrow, ending considerably proximad of junction of dorsal valves with ventral lobes of sheath, thus exposing a lengthy portion of ventral lobes. VENTRAL LOBES OF SHEATH (Figs. 13 E-F; 14 Q-U): lengthily developed proximad of junction with dorsal valves and partly sclerotized there, proximal portion weakly or not at all flanged; greatly elongated distad of junction into two approximate finger-like structures which often project along their entire length at a variable angle from ventral valves; in lateral view (Fig. 13 E), apical third of lobes usually *strongly oblique-truncate (appearing bent slightly ventrad), sometimes apical third rounded or rounded-truncate, ventro-proximal portion with an arcuate enlargement provided with an elongate sclerite (process of ramus of cingulum) on either side; in distal view (Figs. 15 I-J), thick, apices briefly compressed, but depressed and twisted outward so that rims form a V, attingent or *separated below, never appressed, ventro-proximal enlarged portion somewhat keel-shaped. BURSA COPULATRIX AND THICK TUBE (Figs. 18 A-C, G-I): bursa moderately elongate (length 1.9-2.8 (-3.1?) times width), strongly sclerotized; in cross section, concave dorsally, convex ventrally; sclerotization

---

[8]From the Greek, *kontilus*, diminutive of long pole, in facetious allusion to this species' elongate aedeagus which is, however, shorter than in other members of the Psolus Group.

TABLE 7

SIMILARITIES OF *BARYTETTIX CONTILUS TECTATUS* TO *B. PSOLUS* AND OTHER *B. CONTILUS* SUBSPECIES

Character	psolus	contilus tectatus	Other contilus subspecies
DORSAL VALVES (Fig. 14)			
Inner margins	Obtuse angulate, not produced	Obtuse angulate, not produced	Obtuse to acute angulate, always at least slightly produced
Lateral margins	Sub-parallel	Sub-parallel	Divergent or convex
Impression into ventral valves	Yes	No	No
VENTRAL VALVES (Fig. 14)			
Lateral margins	Concave in distal half	Concave in middle or distal half	Sub-parallel, convex, or concave in proximal half
Ventral surface	Keeled or flat proximad, concave distad	Keeled mediad, sometimes weakly concave distad	Sometimes weakly keeled, often lengthily concave
Phallotreme	Narrowly visible from above	Broadly visible from above	Broadly visible from above
LENGTH OF VENTRAL VALVE/ LENGTH OF PRONOTUM	0.23-0.26	0.19	0.19-0.23
LENGTH/WIDTH OF AEDEAGUS	2.6-3.0	1.6	1.6-1.9
BURSA COPULATRIX (Fig. 18)			
Distal sclerite	Proximally pigmented Not pleated at apex Apparently divided	Proximally pigmented Not pleated at apex Apparently divided	Distally pigmented Pleated at apex Apparently continuous across bursa
THICK TUBE (Fig. 18)			
Length of proximal bends	2/3 length of bursa	1/3 length of bursa	1/3 length of bursa
Dilation	Strong	Weak	Absent
Origin	Disto-ventrad	Subdisto-ventrad	Disto-ventrad

divided into proximal and distal portions by a colorless flexible area, proximal sclerotization strongly pleated dorso-laterally and appearing weak or colorless along mid-line, distal sclerotization usually short, apical, variously pigmented, strongly pleated distad and usually extending across bursa (in *c. tectatus*, distal sclerotization long, interrupted along mid-line, pigmented proximad); in lateral view (Figs. 18 A-C), roof of bursa more or less straight almost to apex; thick tube arising ventrally, narrow at origin (but wider than in Humphreysii Group), thence narrowing (except in *c. tectatus* which has a slight proximal dilation), proceeding ventro-caudad to first bend, proximal bends about one-third the length of bursa. COLORATION: ground color light to blackish brown (moderately dark in holotype) with varying amounts of yellow. Head with distinct, usually broad yellow post-ocular stripes (narrow in holotype). Pronotum often *entirely brown dorsally but usually with narrow to broad yellow dorso-lateral stripes on pro- and mesozona and often extending to caudal margin; dorso-longitudinal black band of lateral lobes usually lighter and narrower on metazona (sometimes barely visible there), and usually almost broken by a conspicuous diagonal yellow line on prozona (in San Ignacio colonies of *similis,* this band often complete across entire lobe and almost uniform in width), horizontal yellow line in mesozonal portion of band rarely present, then weakly indicated; ventral half of lateral lobes largely yellow (at least on prozona); ventral carina largely black. Abdomen with mid-dorsal stripe often present but usually weakly defined (absent in holotype); dorso-lateral yellow markings often absent or *obscured, narrow when present; dorso-lateral black spots present, but usually not prominent; tip of abdomen often tinged with color of hind tibia. Hind femur with pagina yellow in ventral half, black in dorsal half, the black stripe sharply defined; geniculae largely black, often tinged with color of base of tibia. Caudal tibia *unicolored, or bicolored, *red, purple or blue. MEASUREMENTS (in mm): holotype male, see under *contilus contilus.* Measurements of the series studied are summarized in Figures 19 and 20.

PARATYPES.— Other than holotypes and juveniles, all specimens examined in this study are designated as paratypes. Male and female paratypes of all subspecies are deposited in the University of Michigan Museum of Zoology, and of all except *c. hiscatus* in the Academy of Natural Sciences of Philadelphia, the United Station National Museum, the British Museum (Natural History), and the Instituto de Biología, Universidad Nacional de México.

TAXONOMIC STATUS.— We have erected this species to include five allopatric populations in the Culiacán region, all of which possess the distinctive feature of a widely open phallotreme. This characteristic is the result of the lateral or medial position of the dorsal edge of the phallotreme wall making the lateral and ventral walls broadly visible from above. The five populations also share a relatively short aedeagus and bursa copulatrix, shorter than other members of the Psolus Group, thicker and more twisted apices of the ventral lobe of the sheath, and short, undilated proximal bends of the thick tube. On the other hand, the populations differ markedly among themselves in the shape of the dorsal aedeagal valves, in details of the ventral valves

and the bursa, and in hind tibial color. With one exception (the dorsal valves in the Tepuche colony), each population is relatively uniform in all aedeagal characteristics. Each population is presently known from a single, or a few adjacent localities, and separated from the next by less than 21 miles. We have grouped these populations into a single species to emphasize the shared distinctive open phallotreme, and short aedeagus and bursa, and we have designated each population as a subspecies to emphasize their allopatry and the uniformity within the populations of the morphological differences between them, although we have no evidence of reproductive compatibility or isolation. The differences between the subspecies are summarized in Table 8.

HABITAT, ASSOCIATED SPECIES, AND SEASONAL OCCURRENCE.— Each of the subspecies of *contilus* has been found in moderately tall, but thinned thorn forest with a moderate growth of bushes in the shade and a good growth of weeds in the sun. In all but one instance (see under *tectatus*), each subspecies has been found with *paloviridis* in the same habitat and often the same bush, and the southernmost subspecies (*similis*) with *poecilus* as well. Our earliest record for the species is 28 July (*similis*) when most adults were teneral and late instar nymphs common, and the latest, 28 November (*similis*) when both males and females were present. Other early and late records are 30 July (*tectatus*), 13 November (*contilus*) and 16 November (*tectatus*).

DISTRIBUTION AND RECORDS.— This species ranges from 3.1 mi NE Tepuche (13.6 mi N Culiacán) to 2 mi N San Ignacio Ferry, Sinaloa. Material examined: 105♂♂, 103♀♀, and numerous juveniles reared to maturity. For a complete list of records see Table 19, p. 104.

Barytettix contilus contilus n. ssp.
Figs. 6 FF; 14 A, I, Q; 15 I; 18 B, H

HOLOTYPE.— ♂, México, Sinaloa, 3 mi NE Tepuche (13.5 mi N Culiacán), 6 September 1966 (T. J. Cohn No. 40); University of Michigan Museum of Zoology.

DIAGNOSIS.— See Table 8 in the discussion of the species.

SUBSPECIES DESCRIPTION (invariable characters, condition in holotype indicated by asterisk preceding that condition).— CERCUS (Fig. 6 FF): dorsal margin weakly concave, disto-dorsal portion weakly enlarged, disto-ventral tooth moderately produced. AEDEAGUS (Figs. 14 A, I, Q): narrow in comparison with other *contilus* subspecies (length 1.8 times median width). DORSAL VALVES: in cephalic view (Fig. 14 A), rounded from side to side, appressed to ventral valves, sometimes *with a hump on each free lobe, medial margins of free

TABLE 8

COMPARISON OF *BARYTETTIX CONTILUS* SUBSPECIES

Character	contilus	tectatus	hiscatus	dicranatus	vumlis
DORSAL VALVES					
Medial margin angulation (Figs. 14 A-E)	Acute or rectangulate	Broadly obtuse angulate, not produced	Rectangulate, slightly produced	Narrow finger-like projections	Obtuse angulate, slightly produced
Shape from side to side	Rounded, appressed	Rooflike and flaring	Rounded dorsally, flaring ventrally	Rounded, appressed except distally	Rounded, appressed
Dorsal hump	Sometimes two distad	Single, prominent, median	None	Two, distad	None
Ventral margin in side view	Sinuate	Straight	Straight	Weakly concave	Sinuate
VENTRAL VALVES					
Lateral margin in side view (proximal 2/3)	Exposed	Obscured	Broadly exposed (Fig. 13 E)	Exposed	Barely exposed, all or part
Dorsal ridge (Figs. 14 A-E)	Sharp, medial, diverging proximad	Blunt, lateral (entire lateral margin elevated), converging, then parallel proximad	Blunt, lateral, converging proximad	Sharp, medial, diverging proximad	Blunt or sharp, lateral, converging proximad
Lateral margin (Figs. 14 I-M)	Weakly convex	Concave	Parallel	Broadly concave proximally, convex distally	Sinuately convex
Ventral surface (Figs. 14 I-M)	Flat or weakly concave	Keeled in middle; flat, convex, or concave distally	Weakly keeled proximally, weakly concave distally	Weakly keeled proximally, concave in middle, flat distally	Distal 2/3 strongly concave, flatter proximad
BURSA COPULATRIX					
Distal sclerite (Figs. 18 A-C, G-I)	Pigmented and strongly pleated subdistally	Pigmented proximally, not pleated distally	Pigmented and strongly pleated subdistally	Pigmented and strongly pleated subdistally	Pigmented and moderately pleated distally
Thick tube (Figs 18 A-C, G-I)	Origin disto-ventral, not dilated	Origin subdisto-ventral, dilated	Origin disto-ventral, not dilated	Origin disto-ventral, not dilated	Origin disto-ventral, not dilated
TIBIAL COLOR	Red	Bluish	Bluish	Bluish, purplish, wine or red	Red or purplish

lobes parallel proximad, forming a narrow U, then each margin with a rounded rectangulate or *acute angulate tooth, this usually *shorter, but sometimes as long as lateral apical tooth, never finger-like, the excision between dorsal and lateral teeth always shallow, lateral margins of valves diverging slightly distad to near apex, then weakly converging to apex; in side view, ventro-lateral margin weakly sinuate, exposing lateral portion of ventral valve, apex broadly rounded, hardly produced. VENTRAL VALVES: in cephalic view (Fig. 14 A), dorsal ridge usually sharp, arising at apex of valve or *near inner margin slightly behind apex, proceeding proximad along mid-line, the ridges usually diverging slightly before disappearing under dorsal valves; in side view, ventro-lateral margins weakly and broadly sinuate; in caudal view (Fig. 14 I), lateral margins sub-parallel to near middle, then converging gradually to *narrowly blunt or sharp acute apices (longer than those in *c. similis*), ventral surface *almost flat or weakly longitudinally concave. BURSA COPULATRIX (Figs. 18 B, H): distal sclerotization short, apical, pigmented subdistally across bursa, and strongly pleated; thick tube arising ventrally, immediately proximad of apex, without dilations. COLORATION: in dried specimens ground color varying from light to *dark brown, dull colored above. Hind tibia *entirely bright red in dark specimens, lighter in specimens with lighter ground color, almost orange in one light individual (probably faded or poorly preserved). MEASUREMENTS (in mm): male holotype: length of body, 32.13; length of pronotum, 6.87; length of tegmen, 5.20; length of fore femur, 6.25; length of hind femur, 16.91; maximum width hind femur, 4.45. Measurements of the series studied are summarized in Figures 19 and 20.

DISTRIBUTION.— Known only from a few localities about 3 mi N of Tepuche (about 13 mi N Culiacán).

RECORDS.— Specimens examined: 24♂♂, 26♀♀, several juveniles reared to maturity. All records are listed in Table 19, p. 104

Barytettix contilus tectatus[9] n. ssp.
Figs. 6 GG; 14 B, J, R; 18 C, I

HOLOTYPE.— ♂, México, Sinaloa, 9 mi SE Culiacán, 16 November 1958 (T. J. Cohn No. 288); University of Michigan Museum of Zoology.

DIAGNOSIS.— See Table 8 in the discussion of the species, and Table 7 comparing this subspecies with *B. psolus.*

SUBSPECIES DESCRIPTION (in variable characters, condition in holotype indicated by asterisk preceding that condition).— CERCUS (Fig. 6 GG): dorsal margin barely or *not at all concave, disto-dorsal portion not enlarged, disto-ventral tooth moderately produced. AEDEAGUS (Figs. 14 B, J, R): broad in comparison with other *contilus* subspecies (length 1.6 times median width). DORSAL VALVES: in cephalic view (Fig. 14 B), roof-like, with a broad median hump proximad of free lobes, medial margins of free lobes parallel or *subparallel a variable distance proximad, forming a narrow U, then diverging evenly to lateral apices, angle of medial margin broadly obtuse, lateral margins of valves almost straight or *weakly flared in middle; in side view, ventro-lateral margin almost straight, completely obscuring all but apices of lateral margins of ventral valve, apex of dorsal valve blunt acute, lying on dorso-lateral surface of ventral valve; in caudal view (Fig. 14 J), extending far laterad of ventral valves. VENTRAL VALVES: in cephalic view (Fig. 14 B), lateral mar-

gins strongly elevated proximad of apex, strongly converging proximad as high, blunt ridges, then proceeding parallel, but not touching until covered by dorsal valves, parallel portions sometimes *covered by dorsal valves; in lateral view, ventro-lateral margin invisible except for upturned apical portion, medial margin visible, broadly convex; in caudal view (Fig. 14 J), lateral margins broadly and weakly concave to near apex, then converging to short, sharp acute apices, ventral surface keeled in middle (broadly V-shaped in cross section), variously flat, *convex or concave distally. BURSA COPULATRIX (Figs. 18 C, I): distal sclerotization long, unpigmented along mid-line, pigmented proximad, thickly sclerotized to apex, not pleated distad; thick tube arising subdistally (more proximad than in other *contilus* subspecies) and with a moderate dilation in proximal bend region. COLORATION: ground color light to blackish brown (moderately dark in holotype), with prominent post-ocular and dorsal pronotal yellow stripes. Hind tibia dull blue, often *with a slight purplish cast distad. MEASUREMENTS (in mm): holotype male: length of body, 34.26; length of pronotum, 6.93; length of tegmen, 5.19; length of fore femur, 6.22; length of hind femur, 17.99; maximum width of hind femur, 4.87. Measurements of the series studied are summarized in Figures 19 and 20.

HABITAT AND ASSOCIATED SPECIES.— We have collected this subspecies only at the base and summit of Cerro Tule, seven to nine miles south of Culiacán. In both places it occurs in heavy weeds and ecotonal plant growth at the edge of the thorn forest, and more sparsely within the forest proper. It is found alone at the top, but occurs sympatrically with *paloviridis* at the bottom of the mountain. Cerro Tule appears to be clothed with a rich thorn forest, broken only by the long narrow road to a micro-wave station at its summit. The forest has probably been little disturbed except for limited lumbering.

The presence of *tectatus* at the summit and the conspicuous absence there of the widespread and common *paloviridis* suggests that *tectatus* is more a denizen of bushy perennials and low growth of forest reproduction than of the more herbaceous and grassy environs to which *paloviridis* is partial. This may explain the geographic restriction of *tectatus* and the other four *contilus* subspecies. These forms may be unable to penetrate very far into open and disturbed habitats because of environmental factors operating on nymphs and adults, or species requirements for oviposition, or exclusion from these environs by interaction with *paloviridis*. We have not investigated any of these factors. Owing to the probable sparsity of *tectatus* throughout the forest, it may be difficult to demonstrate the manner of its penetration to the summit. We suspect that movement was made possible by the creation of localized ecotonal conditions resulting from major disturbances such as fire or wind.

DISTRIBUTION.— Known only from Cerro

---

[9]From the Latin, *tectum*, roof, in allusion to the roof-like dorsal valves of the aedeagus.

Tule, 7-9 mi SE Culiacán. Adjacent wooded hills have been inadequately sampled, and only the edges of flat-land thorn forest have been investigated between Cerro Tule and 23 mi SE Culiacán where *dicranatus* has been found. We also have a few specimens labelled as from 15 mi N Culiacán collected by Cohn and E. R. Tinkham, which locality we believe to be in error. The specimens so labelled do not correspond with the numbers and description of the *Barytettix* from this locality in Cohn's field notebook. Collections made immediately previous to this one were just south of the Río Culiacán in the known range of *tectatus*, and specimens and field notes for this locality again do not correspond. We have failed in several attempts to locate a *tectatus* colony 15 miles north of Culiacán or at other nearby localities.

RECORDS.— Material examined: 12 ♂♂, 7 ♀♀, and a number of juveniles reared to maturity. Localities are listed in Table 19, p. 104.

Barytettix contilus hiscatus [10] n. ssp.
Figs. 6 HH; 13 E-F; 14 C, K, S; 15 J

HOLOTYPE.— ♂, México, Sinaloa, 19.9 mi SE Culiacán on Hwy. 15, 280 ft., 31 August 1961 (I. J. Cantrall and T. J. Cohn No. 59); University of Michigan Museum of Zoology.

DIAGNOSIS.— See Table 8 in the discussion of the subspecies.

SUBSPECIES DESCRIPTION.— CERCUS (Fig. 6 HH): dorsal margin weakly concave, disto-dorsal portion weakly enlarged, disto-ventral tooth moderately produced. AEDEAGUS (Figs. 13 E-F; 14 C, K, S): medially narrow in comparison with other *contilus* subspecies (length 1.8 times median width). DORSAL VALVES: in cephalic view (Fig. 14 C), rounded from side to side dorsally, then flaring, without a dorsal hump, medial margins of free lobes parallel proximad, forming a long narrow U, then each margin with a slightly produced, rounded, rectangulate lobe before diverging to lateral apices, lateral margins sub-parallel in proximal half, then weakly convex in distal half; in side view (Fig. 13 E), ventro-lateral margin almost straight, broadly exposing lateral margin of ventral valve, apex blunt acute. VENTRAL VALVES: in cephalic view (Fig. 14 C), dorsal ridge strong, blunt, arising near, but not on lateral margin of each valve, the ridges converging slightly proximad, but remaining lateral until obscured by dorsal valves; in side view (Fig. 13 E), ventro-lateral margin almost straight; in caudal view (Fig. 14 K), lateral margins sub-parallel to near apex, then briefly rounded mediad to short, broad, blunt-acute apices; ventral surface weakly concave distad, weakly keeled proximad (broadly V-shaped in cross-section). BURSA COPULATRIX as in *c. contilus* (see Figs. 18 B, H): distal sclerotization short, apical, pigmented subdistally across bursa, and strongly pleated; thick tube arising ventrally, immediately proximad of apex, without dilations. COLORATION: ground color dark brown with prominent or moderately developed post-ocular and dorsal pronotal yellow stripes. Hind tibia dull blue with a faint purplish cast distad. MEASUREMENTS (in mm): holotype male: length of body, 34.58; length of pronotum, 7.44; length of tegmen, 5.11; length of fore femur, 6.23; length of hind femur, 18.24; maximum width of hind femur, 4.63. Measurements of the series studied are summarized in Figures 19 and 20.

DISTRIBUTION AND RECORDS.— Specimens examined: 1 ♂, 1 ♀. SINALOA: 19.9 mi SE Culiacán on Hwy. 15. A careful search was made for this subspecies in 1970, and although *paloviridis* was common throughout the region, and other *contilus* subspecies were common elsewhere, *hiscatus* was not found. Our field notes indicate that the pair was collected in copula at the edge of dense thorn forest; now the area is mostly cleared. The subspecies probably still occurs in thorn forest which we have not investigated east and west of the main road. The type locality is only about three miles northwest of the northernmost colony of *dicranatus* with no obvious barrier separating them.

Barytettix contilus discranatus [11] n. ssp.
Figs. 6 II; 14 D, L, T

HOLOTYPE.— ♂, México, Sinaloa, 30 mi S Culiacán on Hwy. 15, 30 August 1965 (T. J. Cohn No. 85); University of Michigan Museum of Zoology.

DIAGNOSIS.— See Table 8 in the discussion of the species.

SUBSPECIES DESCRIPTION (in variable characters, condition in holotype is indicated by asterisk preceding that condition).— CERCUS (Fig. 6 II): dorsal margin weakly to *moderately concave, disto-dorsal portion weakly to *moderately enlarged, disto-ventral tooth moderately produced. AEDEAGUS (Figs. 14 D, L, T): broad in comparison with other *contilus* subspecies (length 1.6 times median width). DORSAL VALVES: in cephalic view (Fig. 14 D), rounded from side to side, strongly appressed to ventral valves, free lobes each with a hump, medial margins of lobes lengthily parallel or converging slightly distad, apices of lobes deeply excised producing two subequal, tapering, blunt, finger-like projections, one dorsal, the other ventro-lateral, lateral margins flaring slightly and irregularly distad to ventro-lateral apices; in side view, ventro-lateral margin broadly and weakly concave, exposing lateral margin of ventral valve. VENTRAL VALVES: in cephalic view (Fig. 14 D), dorsal ridges sharp, arising near inner margin of each valve near apex, diverging slightly proximad, and proceeding along mid-line of each valve until obscured by dorsal valves; in side view, ventro-lateral margin broadly sinuate; in caudal view (Fig. 14 L), lateral margins broadly concave in proximal half, thence convex, sometimes angulately so, distal third gradually converging to moderately long, sharp acute apices, medial margins *gradually diverging from middle, or distal third concave, ventral surface *moder-

---

[10]From the Latin, *hisco*, open, in allusion to the dorsally open phallotreme.

[11]From the Greek, *dikranon*, pitchfork, in allusion to the toothed dorsal aedeagal valves.

ately longitudinally concave in middle, sometimes strongly so, with lateral margins more strongly bent ventrad than medial margins, surface more or less flat distad, and rounded from side to side or *weakly keeled proximad (broadly V-shaped in cross section). BURSA COPULATRIX: as in *c. contilus* (see Figs. 18 B, H): distal sclerotization short, apical, pigmented subdistally across bursa, and strongly pleated; thick tube arising ventrally, immediately proximad of apex, without dilations. COLORATION: ground color blackish brown, with moderately developed post-ocular and dorsal pronotal yellow stripes. Hind tibia bluish purple, *purple, wine-red, or red, or various combinations of those colors except red. MEASUREMENTS (in mm): holotype male: length of body, 33.61; length of pronotum, 6.72; length of tegmen, 5.08; length of fore femur, 6.14; length of hind femur, 18.5; maximum width of hind femur, 4.84. Measurements of the series studied are summarized in Figures 19 and 20.

GEOGRAPHIC VARIATIONS.— In the colony of this subspecies closest to *c. hiscatus,* only four miles away, we find no tendencies toward aedeagal conditions in that subspecies. However, in leg color, the adjacent *dicranatus* colony not only averages bluer, but several specimens have tibial color almost indistinguishable from that of *hiscatus* (Table 9). Variation is continuous in tibial color and the tabulation is but a crude estimate of the trends in the two colonies. The Sanalona colony has bright red tibiae, much as in *c. contilus* found about 13 miles to the north.

DISTRIBUTION.— This subspecies is known from near Sanalona (east of Culiacán) and from 23-30 mi S Culiacán. South of the southernmost locality, suitable habitats have been investigated without finding *dicranatus,* although *paloviridis* has been found commonly. The northwestern limits and geographic relationship with the nearby *hiscatus* have not been accurately determined, nor has the region east of the main highway been investigated except on the Sanalona and Tepuche roads.

ASSOCIATED SPECIES — As with all other *contilus* subspecies, *dicranatus* is found in the same habitat as *paloviridis.* Cohn's impression while collecting the two was that there was a slight difference in habitat preference. This would be interesting to investigate further in view of the marked shift in the genitalic variation of the *paloviridis* colony which is sympatric with *dicranatus.* This is the only *paloviridis* colony showing such a shift south of the Río Culiacán, although *paloviridis* occurs with each of the other subspecies of *contilus.* This subject is fully discussed under *paloviridis.*

RECORDS.— Specimens examined: 34♂♂, 22♀♀, and several juveniles reared to maturity. Localities are listed in Table 19, p. 104.

Barytettix contilus similis [12] n. ssp.
Figs. 6 JJ; 14 E, M, U; 18 A, G

HOLOTYPE.— ♂, México, Sinaloa, 66 mi SE Culiacán, 6 November 1958 (T. J. Cohn No. 258); University of Michigan Museum of Zoology.

DIAGNOSIS.— See Table 8 in the discussion of the species.

SUBSPECIES DESCRIPTION (in variable characters, condition in holotype indicated by asterisk preceding that condition).— CERUS (Fig. 6 JJ): dorsal margin barely to *weakly concave; disto-dorsal portion *weakly, sometimes moderately enlarged; disto-ventral tooth moderately produced. AEDEAGUS (Figs. 14 E, M, U): medially narrow in comparison with other *contilus* subspecies (length 1.9 times median width). DORSAL VALVES: in cephalic view (Fig. 14 E), rounded from side to side, appressed to ventral valves, without dorsal hump, medial margins parallel proximad for varying distance, forming a narrow U, each margin then forming a *gently rounded or truncate obtuse angle before continuing to lateral apex, lateral margins broadly convex in distal half, weakly divergent in proximal half; in side view, ventro-lateral margin broadly and weakly sinuate, barely exposing *part or all of lateral margin of ventral valve. VENTRAL VALVES: in cephalic view (Fig. 14 E), dorsal ridge *blunt, sometimes sharp, arising *on or near lateral margin subapically, converging slightly proximad and proceeding along midline of each valve until obscured by dorsal valves; in side view, ventro-lateral margins sinuate; in caudal view (Fig. 14 M), lateral margins straight or *weakly diverging to near middle, then margins converging gradually and sinuately to long acute apices (shorter than in *c. contilus*), ventral surface strongly longitudinally concave in distal two-thirds, becoming flatter proximad. BURSA COPULATRIX (Figs. 18 A, G): distal sclerotization short, apical, pigmented distally across bursa and around thick tube origin, moderately pleated (less so than in *c. contilus*); thick tube arising ventrally immediately proximad of apex, without dilations. COLORATION: ground color moderately dark brown, post-ocular yellow stripes wide, dorsum of pronotum and abdomen *dull brown in northern colony, or usually with bright, wide yellow lateral stripes in Elota colony. Hind tibia completely bright *red or orange-red in northern and San Ignacio colonies, reddish purple with bluish at proximal end and on genicular lobes in Elota colony. MEASUREMENTS (in mm): holotype male: length of body, 31.42; length of pronotum, 6.17; length of tegmen, 5.24; length of fore femur, 5.63; length of hind femur, 16.76; maximum width hind femur, 4.24. Measurements of the series studied are summarized in Figures 19 and 20.

GEOGRAPHIC VARIATION.— The two northern colonies of this subspecies, one collected in November, the other in August, are strikingly different from one another in the amount of yellow on the body and the color of the tibia (see above description). The duller body color is similar to that of *c. contilus,* also collected in November. However, earlier collections of that subspecies are similarly dull, and aging can hardly explain the difference in tibial color. The two northern colonies are only about eight miles

---

[12]From the Latin, *similis,* like or resembling, in allusion to the similarity of this subspecies to *c. contilus,* but separated from it by three other *contilus* subspecies.

TABLE 9

TIBIAL COLOR VARIATION IN *BARYTETTIX CONTILUS DICRANATUS* AND *B. C. HISCATUS*

Localities	Wine Red	Purplish Red	Reddish Purple	Purple	Bluish Purple	Blue
hiscatus 19.9 mi SE Culiacán	—	—	—	—	2	—
dicranatus 23.9 mi SE Culiacán	—	—	6	9	8	1
dicranatus 30 mi SE Culiacán	1	1	7	3	—	—

apart; the precise distance is not known because of the discrepancies in speedometer readings upon which a comparison of the distances is based.

ASSOCIATED SPECIES.— At all localities *poecilus* and *paloviridis* were present. *Poecilus* was apparently common, and *paloviridis* rare at the northernmost locality; the reverse was true at the Elota locality.

DISTRIBUTION.— Known from a few localities from 64 to 73 mi SE Culiacán, and from San Ignacio about 90 mi SE Culiacán. Thorough investigation of thorn forest elsewhere in this region has not been made, although we have numerous collections from ruderal habitats containing only *paloviridis* or *poecilus*.

RECORDS.— Specimens examined: 35 ♂♂, 21 ♀♀, and a number of juveniles reared to maturity. Localities are listed in Table 19, p. 104.

Barytettix psolus [13] n. sp.
Frontispiece; Figs. 6 EE; 13 C-D; 14 G, O, W; 15 O, R; 18 D, J

HOLOTYPE.— ♂, México, Sinaloa, 6 mi W Jesús María (19 mi N Culiacán on Presa Humaya [= Presa Adolpho Lopez Mateos] Road), 11 November 1958 (T. J. Cohn No. 279); University of Michigan Museum of Zoology.

DIAGNOSIS.— *Psolus* is the only species of *Barytettix* in which the dorsal aedeagal valves are impressed into the surface of the ventral valves, usually creating a low ridge just distad of

the end of the dorsal valves. The brown ground color, pronotal and femoral color pattern, elongate aedeagus, and elongate bursa copulatrix distinguish *psolus* from all but *nigrofasciatus* (Table 6, p. 34). The elongate aedeagus is indicated by the sac-like enlargement of the pallium, as in all members of the Psolus Group (similar to Fig. 15 H). *Psolus* differs from *nigrofasciatus* in the male by the shape of the dorsal valves (compare Figs. 13 C and 14 G with 15 E and 14 H) and by the sculptured ventral surface of the ventral valves (compare 13 D and 14 O with 14 P) and in the female by the straight disto-dorsal margin and longitudinally divided distal sclerite of the bursa (Fig. 18 D, J). Further comparisons are made in Table 6.

Color comparison of all species of the genus may be found in Table 3, p. 25.

Psolus may be distinguished by color from *contilus* and *nigrofasciatus* only by the geography of various of the color features. This is discussed below under geographic variation, and tibial color comparisons are made in Table 11. In pronotal and femoral color pattern, *psolus* and *contilus* are identical. *Psolus* is different in both of these characters from *nigrofasciatus* throughout most of the range of the former, but, except in tibial color, Cosalá specimens of *psolus* are almost identical to San Ignacio individuals of *nigrofasciatus*.

Within the Psolus Group as well as within the genus, *psolus*, *contilus* and *nigrofasciatus* form a distinctive subgroup in pronotal, femoral and ground color characteristics, in the shape of the ventral lobe of the aedeagal sheath in side view,

[13]From the Greek, *psolos*, circumcized, in allusion to the seemingly cut-back dorsal valves and strangulate ventral valves of the aedeagus.

the position of the dorsal aedeagal valves, and in the disto-ventral or ventral origin of the thick tube of the receptaculum seminis (Table 6, p. 34). *Psolus* is more similar to *nigrofasciatus* than it is to *contilus* in the longer aedeagus, longer bursa, dilations of the thick tube, more proximal position of the distal sclerite of the bursa, disto-ventral origin of the thick tube and almost invisible phallotreme walls in dorsal view. The first three characteristics are also found in *paloviridis*. In most southern populations of *paloviridis* which are allopatric to *psolus* the slight exposure of the phallotreme (compare Figs. 15 Q and R) and the sculpturing of the ventral surface of the ventral valves are remarkably similar to *psolus*. The bursa of *contilus tectatus* is similar to that of *psolus* (Table 7) except in the position of the origin of the thick tube (Figs. 18 J and I). These comparisons are summarized in Table 6, p. 34), and their phylogenetic implications are discussed in a later section on the relationships of all *Barytettix* species.

SPECIES DESCRIPTION (in variable characters, condition in holotype is indicated by asterisk preceding that condition).— CERCUS (Fig. 6 EE): dorsal margin *almost straight to moderately concave; disto-dorsal portion not at all, to *slightly enlarged; disto-ventral tooth *moderately to strongly produced, acute. AEDEAGUS (Figs. 13 C-D; 14 G, O, W; 15 O, R): elongate (0.23-0.26 times length of pronotum), and very narrow (length 2.6-3.0 times mid-dorsal width). DORSAL VALVES: in cephalic view (Figs. 14 G, 15 R), usually smoothly rounded from side to side, more or less appressed to ventral valves and impressed into their surface distally, medial margins of free lobes proximally parallel and forming a narrow U, then diverging smoothly at obtuse but not produced angles to latero-ventral rounded apices, medial margins rarely arcuately diverging from base, proximal fused portion usually *medially flat, sometimes broadly and weakly swollen, never with a distinct hump, lateral margins of valves sub-parallel; in lateral view (Fig. 13 C), ventro-lateral margin straight for most of length, often *curving slightly dorsad near apex, usually covering lateral margin of ventral valve. VENTRAL VALVES: in cephalic view (Figs. 14 G, 15 R), with dorsal valves appearing impressed into surface, sometimes with a low swelling just distad of apices of dorsal valves, visible surface convex, lateral walls of phallotreme narrowly visible at least distally; in lateral view (Fig. 13 C), lateral margin usually covered by dorsal valve, but much of ventral surface usually visible, ventro-lateral margin straight in proximal half, distinctly but shallowly concave at and just beyond apex of dorsal valve, then slightly convex to apex, valves in this view thick at apex of dorsal valve and tapering rapidly distad; in caudal view (Figs. 13 D, 14 O), medial margins touching in proximal third, then diverging gradually and becoming *sub-parallel or converging slightly distad, lateral margins sinuate, but always with a distinct shallow concavity at distal third just proximad of apices of dorsal valves, ventral surface *weakly keeled, convex across both valves, or flat in proximal third, with a lateral longitudinal swelling near middle third, and usually distinctly concave in distal quarter, this portion of valve appearing slightly twisted inward. RAMUS OF CINGULUM (similar to Figs. 1 C-D): ventro-distal portion narrow, ending considerably proximad of junction of dorsal valves with ventral lobes of sheath, thus exposing a lengthy portion of ventral lobes. VENTRAL LOBES OF SHEATH (Figs. 13 C-D, 14 W): lengthily developed proximad of junction with dorsal valves and partly sclerotized there, proximal portion slightly or not at all flanged; greatly elongated distad of junction into two approximate, finger-like structures which often project along their entire length at a variable angle from ventral valves, rarely appressed to valves; in lateral view (Fig. 13 C), dorsal margin usually slightly convex at least distad, rarely straight, apices variously round or *truncate, sometimes almost squarely truncate, ventro-proximal portion with a large arcuate enlargement provided with an elongate sclerite (process of ramus of cingulum) on either side; in distal view (Fig. 15 O), apices *more or less oval, often depressed and twisted, sometimes with narrow outer rims forming a V, touching or open below as in *contilus*, never appressed, ventro-proximal enlarged portion somewhat keel-shaped, often narrow. BURSA COPULATRIX AND THICK TUBE (Figs. 18 D, J): bursa elongate (length 3.5 times width), strongly sclerotized; in cross section concave dorsally, convex ventrally; sclerotization divided into proximal and distal sclerites by a colorless flexible area, proximal sclerite strongly pleated dorso-laterally, and appearing weak and colorless along mid-line, distal sclerite pigmented and pleated proximally, interrupted along midline by a narrow, colorless area, thick sclerotization extending to apex of bursa, but not pigmented distally; in lateral view (Fig. 18 D), roof of bursa more or less straight to apex; thick tube arising disto-ventrad and proceeding ventrocaudad to first bend, proximal bends about two-thirds the length of bursa, each with a relatively small bladder-like dilation. COLORATION (Frontispiece): ground color light to dark brown (moderate in holotype), blackish in south, with a variable amount of yellow. Head with *narrow to wide yellow postocular stripes. Pronotum with dorso-lateral yellow stripes wide, *narrow or absent, when present sometimes not extending onto metazona or lighter there; dorso-longitudinal black band of lateral lobes usually lighter and narrower on metazona (sometimes barely visible there), and usually almost broken by a conspicuous diagonal yellow line on prozona (in Cosalá specimens, this band often complete across entire lobe and almost uniform in width), horizontal yellow line in band in mesozona rarely present; ventral half of lateral lobes yellow, ventral carina largely black. Abdomen with mid-dorsal yellow stripe well-defined in light specimens, *absent in dark ones; dorso-lateral yellow spots wide and prominent in light specimens, weak or *absent in darker specimens; dorso-lateral black spots prominent; tip of abdomen usually concolorous with the rest, sometimes tinged with color of proximal portion of hind tibiae. Hind femur with pagina yellow in ventral half, jet black in dorsal half, the black stripe sharply defined; geniculae with *black or brownish lunae, and blue ventral half (reddish or orange at Cosalá). Hind tibia proximally blue (reddish at Cosalá), distally bluish with a slight purplish cast in north, grading southward through blue-purple, purple, *wine, to bright red and orange-red, thus *conspicuously bicolored in middle populations but color grading imperceptibly from proximal to distal end of tibia, and unicolored in northernmost and southernmost colonies. MEASUREMENTS (in mm): holotype male: length of body, 33.08; length of pronotum, 6.87; length of tegmen, 4.91; length of fore femur, 5.80; length of hind femur, 17.24; greatest width of hind femur, 4.66. Measurements of the series studied are summarized in Figures 19 and 20.

PARATYPES.— Other than the holotype, all adult specimens examined in this study are designated as paratypes. Male and female paratypes are deposited in the University of Michigan Museum of Zoology, the Academy of Natural Sciences of Philadelphia, the United States National Museum, the British Museum (Natural History), and the Instituto de Biología, Universidad Nacional de México.

GEOGRAPHIC VARIATION.— This species displays marked geographic variation in tibial color which is summarized in Table 10. North of Culiacán we have two sets of collections, one almost forming a transect north to Badiraguato, and another forming a northwest transect to Guamúchil, which lies almost due west of Badiraguato and is separated from it by a small range of mountains. The northwesternmost samples have entirely blue tibiae (under strong light the distal portions are slightly purplish). The distal portion of the tibiae becomes progressively redder southeastward, and the samples contain progressively fewer individuals with all blue tibiae, and more with purple or wine distally. This variation appears to be clinal geographically, and continuous within any one population. Close to Culiacán almost all individuals have the tibiae blue proximally and wine distally. In the northern transect, on the other hand, all individuals have the blue-wine tibiae found only much closer to Culiacán in the northwestern transect. It is interesting to note in this regard that some of the northern colonies must come very close to, or are sympatric with *c. contilus*. These are the colonies with tibial color most similar to the orange-red tibiae of *c. contilus,* which also has a pronotal and femoral color pattern identical to that of *psolus.* These nearby *psolus* colonies show no aedeagal similarities to *contilus.*

The southeasternmost colonies of *psolus* in the vicinity of Cosalá are separated by a wide gap from those north of Culiacán, but their orange-red tibiae may be a continuation of the trend seen in the northwest transect.

The Cosalá colonies are distinctive in two other color characters. Individuals there are much darker than those to the north, and some appear even blackish in life. In addition, some have a continuous black band across the lateral lobes of the pronotum and are thus almost indistinguishable from *nigrofasciatus.* The nearest colony of that species, 35 miles to the southeast at San Ignacio, is very similar in pronotal and femoral color, but has purplish tibiae. Not far east of the Cosalá *psolus* colonies, *contilus similis* is found with similar tibial and femoral color but with the dark bar on the lateral pronotal lobes much lighter on the metazona. The distribution of tibial color of *psolus* and its relatives is summarized in Table 11.

In aedeagal characters, there appears to be more variation within the Cosalá colonies than elsewhere. It is difficult to accurately gauge the extent of this variation because most of the specimens from Cosalá are teneral. This situation might offer additional evidence for the theory of mechanical reproductive isolation developed under *paloviridis* and in a later section of this paper. The *psolus* colonies close to Cosalá appear to be above the altitudinal range of *paloviridis,* and their aedeagal variability might be the result of reduced selective pressure for uniformity in the absence of its close relative. The two species do overlap at lower elevations (19.5 mi SW Cosalá), and a mismated pair has been collected there. Unfortunately we have only two males from that locality, and although they differ somewhat from one another, many more are needed to determine the extent of the aedeagal variability here as a check against that in colonies closer to Cosalá.

HABITAT, ASSOCIATED SPECIES, AND SEASONAL OCCURRENCE.— This species has been found in the weedy-bushy ruderal habitats typical of many *Barytettix* species, but usually at the edge of thorn forest. It has also been collected in bushy overgrown fields, in thinned thorn forest among thin weeds and bushes, and, at its southernmost locality, in thinned but uncultivated tropical deciduous forest. It is apparently absent from more extensively disturbed habitats, such as in the weedy-bushy edges of fields in extensively cultivated areas.

Paloviridis has been found at almost all *psolus* localities. At 14 mi NW Culiacán, there is some indication that *psolus* and *paloviridis* have slightly different habitat preferences or are partially excluding each other from parts of the habitat. There, *psolus* was found only within and at the edge of thinned thorn forest, while *paloviridis* was less common there but abundant in the more weedy open areas. A difference in habitat may also be indicated by the abundance of *psolus* in contrast to the conspicuous absence of *paloviridis* in tall but somewhat thinned thorn forest at 6 mi W Jesús María, and in low, dense thorn forest near Badiraguato. This pattern is not borne out, however, near Culiacán. *Psolus* has not been found at the *paloviridis* type locality, 2.5 mi NW Bridge over Río Culiacán at Culiacán, in heavily thinned thorn forest with abundant weeds and bushes but also with thinner shady areas; yet *psolus* is not uncommon with *paloviridis* on the embankment of the southern end of the railroad bridge at Culiacán only three miles away in an

area of heavy weeds and low bushes largely devoid of trees.

South of Culiacán there appears to be a sharp difference in altitudinal range between the two species. On the Cosalá road, about 69 mi SE Culiacán, *psolus* is common at elevations from 1600 feet around Cosalá, to 700 feet at 19.5 mi SW Cosalá. *Paloviridis* occurs no higher than the latter locality, where it is sympatric with *psolus*, and is common in the nearby lowlands where *psolus* is absent. This is the only region in the range of *psolus* where elevations above that of the coastal plain have been investigated.

In the lowlands between the Cosalá road and Culiacán, *psolus* is apparently completely absent along the main highway, an area which has been intensively searched for *Barytettix* on several occasions. This situation is unexpected in view of the abundance of *psolus* in lowlands immediately north of Culiacán and in the city itself. It is possible that the closely related *contilus* occupies the habitat required by *psolus* in the area south of Culiacán as well as that north of Tepuche. Nowhere does *psolus* occur sympatrically with *contilus*. The known southernmost colonies of *psolus* around Cosalá are found within about 10 miles of *contilus similis*. The Culiacán colony of *psolus* is located only about seven miles from the nearest *contilus tectatus* colony. In the Tepuche region, *psolus* has been found only a mile from the *c. contilus* colony, and a large *psolus* colony was found only five miles to the southwest. Both species occur on the east side of the Río Humaya and there are no obvious barriers between them. Sufficient collecting was done at the *c. contilus* locality to make reasonably certain that *psolus* would have been found had it been present, but inadequate collecting has been done between that locality and the nearest *psolus* colony. All three *contilus* subspecies are found within and at the edge of thorn forest, the habitat preferred by *psolus*. This situation is suggestive of competitive or reproductive exclusion, and may explain the absence of *psolus* from the lowlands south of Culiacán.

Tridens has also been found at a number of *psolus* localities, where the latter has usually been more abundant.

Psolus is known from near sea level on the coastal plain to 1600 feet near Cosalá, the highest elevation investigated within its range.

Our earliest record for the species is 24 August at Cosalá at which time nymphs were abundant.

Late instar nymphs were common on 31 July at 14 mi NW Culiacán, but no adults were found during an intensive search. The latest record is 13 November at Jesús María when the species was common. No collecting for *psolus* has been done earlier or later than the above records.

DISTRIBUTION.— The northwesternmost record for *psolus* is 62 mi NW Culiacán, the northeasternmost, 5.3 mi NW Badiraguato, and the southernmost, 19.5 mi SW Cosalá, all in Sinaloa. The species is apparently absent in the lowlands between the last locality and Culiacán. Inland the foothills and mountains have been investigated only between Sanalona and Los Mayos (east of Culiacán) where only *contilus dicranatus* and *paloviridis* were found.

RECORDS.— Specimens examined: 131 ♂♂, 113 ♀♀, and several juveniles reared to maturity. All localities are listed in Table 19, p. 104.

Barytettix nigrofasciatus [14] n. sp.
Figs. 6 DD; 14 H, P, X; 15 E, K; 18 E, K

HOLOTYPE.— ♂, México, Sinaloa, 8.3 mi SW Santa Lucía [on Durango-Mazatlán Highway], 2740 ft., 27 August 1961 (I. J. Cantrall and T. J. Cohn No. 52); University of Michigan Museum of Zoology.

DIAGNOSIS.— This species may be distinguished from other *Barytettix* species with the exception of *psolus* by the combination of brown ground color, special pronotal markings (Table 6, p. 34), an elongate aedeagus with the walls of the phallotreme almost invisible in dorsal view (Fig. 14 H), and two bladder-like dilations in the thick tube of the receptaculum seminis (Figs. 18 E, K). The elongate aedeagus is indicated in undissected specimens by a sac-like enlargement of the pallium (similar to Fig. 15 H), as in all members of the Psolus Group. From *psolus*, this species may be distinguished by the conspicuous dorso-medial bulge on the dorsal aedeagal valves (Fig. 15 E), and by the undivided distal sclerite and declining distal third of the roof of the bursa copulatrix (Figs. 18 E, K). The combination of a complete dark bar of relatively uniform width across the lateral lobes of the pronotum, and a gray or poorly defined paginal stripe, both found near Concordia (but not at San Ignacio), is unique in the genus. Further comparisons are made in Table 6.

---

[14]From the Latin, *nigro*, black, + *fascia*, ribbon or band, in reference to the broad dark band on the lateral lobes of the pronotum.

TABLE 10

GEOGRAPHIC VARIATION IN THE DISTAL COLOR OF THE HIND TIBIAE IN *BARYTETTIX PSOLUS*

Western Populations					Eastern Populations				
	Blue	Purple	Wine	Red		Blue	Purple	Wine	Red
62, 60 mi NW Culiacán	10	–	–	–	5.4 mi N Badiraguato	–	–	9	–
50 mi NW Culiacán	26	4	–	–					
42 mi NW Culiacán	2	–	–	–					
					6 mi W Jesús María (23 mi N Culiacán)	–	–	17	–
20.7 mi NW Culiacán	7	5	2	–					
					1 mi E San Rafael (13 mi N Culiacán)	–	–	16	–
15.4-15.2 mi NW Culiacán	9	17	3	–					
					*2 mi SW Tepuche (11 mi N Culiacán)	–	–	7	–
					2 mi W Agua Caliente (11 mi N Culiacán)	–	–	7	–
					El Bario (7.5 mi N Culiacán)	–	–	2	–
					*4.7 mi SW Tepuche (5.8 mi N Culiacán)	–	–	4	–
					*3 mi NE Culiacán	–	–	12	–
2 mi NW Río Culiacán	–	1	8	–					
					6.6 mi NE-19.5 mi SW Cosalá	–	–	–	46

*Localities east of the Río Humaya.

Color comparisons of all species of the genus may be found in Table 3, p. 25 . *Nigrofasciatus* may be distinguished by color from *contilus* and *psolus* only by the geography of the various color features, with the exception of the unusual weak paginal stripe in the Concordia colonies. This is discussed under geographic variation of *psolus* and tibial color comparisons are made in Table 11, p. 49 .

Within the Psolus Group as well as within the genus, *nigrofasciatus, psolus* and *contilus* form a distinctive subgroup in pronotal, femoral and ground color, in the shape of the ventral lobe of the aedeagal sheath in side view, the position of the dorsal aedeagal valves, and in the ventral or disto-ventral origin of the thick tube of the re-

TABLE 11

GEOGRAPHIC VARIATION IN THE DISTAL COLOR OF THE HIND TIBIAE

IN THE BROWN MEMBERS OF THE PSOLUS GROUP

AND IN OTHER SPECIES FOUND WITH THEM

Localities[1]	*psolus*[2]	*contilus*	*nigrofasciatus*	Other Species[3]	
62-42 mi NW Culiacán	Blue, purple	—	—	*paloviridis*	wine
5 mi N Badiraguato	Wine	—	—	—	
23-13 mi N Culiacán	Wine	Red, orange-red (*c. contilus*)	—	*tridens*	blue
21-15 mi NW Culiacán	Blue, purple, wine	—	—	*paloviridis* *tridens*	wine blue
9-3 mi N Culiacán	Wine	—	—	*paloviridis*	wine
2 mi NW Culiacán	Wine, purple	—	—	*paloviridis*	wine
7-9 mi SE Culiacán	—	Bluish (*c. tectatus*)	—	*paloviridis* *tridens*	wine blue
20 mi SE Culiacán	—	Bluish (*c. hiscatus*)	—	*paloviridis*	wine
24-30 mi SE Culiacán	—	Bluish-purple, purple, wine (*c. dicranatus*)	—	*paloviridis* *tridens*	wine blue
66-74 mi SE Culiacán	—	Orange-red, red, purplish (*c. similis*)	—	*paloviridis* *poecilus* *tridens*	wine, purple purple blue
7 mi NE to 20 mi SW Cosalá (about 50 mi SE Culiacán) (Foothills above 700 ft.)	Red	—	—	*paloviridis* *tridens*	wine blue
2 mi N to 2 mi SW San Ignacio	—	Orange-red (*c. similis*)	Purplish[4]	*paloviridis* *poecilus*	wine purple
Concordia-Santa Lucía	—	—	Orange	*poecilus*	purple

[1]Mileage rounded to nearest mile.

[2]Except between 62 and 15 mi NW Culiacán where many specimens have entirely blue tibiae, *psolus* is conspicuously bi-colored north of Culiacán, and in this region is always blue proximad whereas *paloviridis* is wine proximad.

[3]*Paloviridis, poecilus* and *tridens* are always unicolored in this entire region. The first two species are always bright green, the third is brown but always with a light brown ventral carina of the lateral lobes of the pronotum (as opposed to the black ventral carina in all brown members of the Psolus Group).

[4]Usually bicolored, darker proximad.

ceptaculum seminis. *Nigrofasciatus* resembles *psolus* more than it does *contilus* in the similarly elongate aedeagus and bursa, almost invisible walls of the phallotreme, dilations of the thick tube, more proximal position of the distal sclerite of the bursa, and a similar shape of the distal portion of the bursa. The first three characteristics are also found in *paloviridis*. On the other hand, the apices of the ventral aedeagal lobes in distal and often in side view in *nigrofasciatus* are almost identical to those in *contilus* and different from the general condition in *psolus*. Further, the *nigrofasciatus* bursa and dorsal aedeagal valves are similar to those of *contilus tectatus*. These comparisons are summarized in Table 6, p. 34 , and their phylogenetic implications are discussed below in a section on the relationships of the members of the genus *Barytettix*.

SPECIES DESCRIPTION (in variable characters, condition in holotype indicated by asterisk preceding that condition).— CERCUS (Fig. 6 DD): dorsal margin *straight to barely concave; disto-dorsal portion *not at all or barely enlarged; disto-ventral tooth moderately produced, acute. AEDEAGUS (Figs. 14 H, P, X; 15 E): very elongate (0.3 times length of pronotum), very narrow (length 2.6-*2.7 times mid-dorsal width). DORSAL VALVES: in cephalic view (Fig. 14 H), proximal half rounded from side to side and appressed to ventral valves, distal half flaring laterad, medial margins of free lobes evenly diverging and forming a V, lateral margins more or less straight, subparallel, apices narrowly rounded and lying on dorso-lateral surface of ventral valves, a prominent medio-dorsal hump present near origin of free lobes; in lateral view (Fig. 15 E), ventral margin straight to weakly sinuate, exposing at least distal half of lateral edge of ventral valve. VENTRAL VALVES: in cephalic view (Fig. 14 H), visible surface more or less flat and sloping laterad, usually with a weak longitudinal ridge near medial margin, apices of valves slightly twisted, lateral walls of phallotreme narrowly visible from above and weakly convex distad; in lateral view (Fig. 15 H), ventro-lateral margin straight or *barely curved ventrad, very briefly and weakly convex distad, valve in this view moderately thick at apex of dorsal valve and tapering evenly to apex; in caudal view (Fig. 14 P), medial margins touching or slightly separated in proximal third of half, then very gradually diverging and becoming sub-parallel or *slightly convergent distad, lateral margins broadly and weakly concave in proximal two-thirds, then gently convex to apices, ventral surface flat, but distal third of valve gently twisted inward. RAMUS OF CINGULUM (similar to Figs. 1 C-D): ventro-distal portion narrow, ending considerably proximad of junction of dorsal valves with ventral lobes of sheath, thus exposing a lengthy portion of ventral lobes. VENTRAL LOBES OF SHEATH (Figs. 14 X, 15 E): lengthily developed proximad of junction with dorsal valves and partly sclerotized there, with a weak to moderate proximal flange; greatly elongated distad of junction into two approximate, finger-like structures which often project along their entire length at a variable angle from ventral valves, or appear lipped in side view; in lateral view (Fig. 15 E), dorsal margin almost straight to *somewhat convex, apices variously rounded or truncate, sometimes *squarely truncate, ventro-proximal portion with a large arcuate enlargement provided with an elongate sclerite (process of ramus of cingulum) on either side; in distal view (Fig. 15 K), apices more or less oval, or thick and trigonal, or *depressed and twisted so that the narrow rims form a V which is *open or closed below, apices never appressed, ventro-proximal

enlarged portion somewhat keel-shaped. BURSA COPULATRIX AND THICK TUBE (Figs. 18 E, K): bursa elongate (length 3.5 times width), strongly sclerotized; in cross section, concave dorsally, convex ventrally; sclerotization divided into proximal and distal sclerites by a colorless flexible area, proximal sclerite strongly pleated dorso-laterally and appearing weak and colorless along mid-line, distal sclerite pigmented and pleated proximally, unbroken across bursa, pigmented area rounded distally, distal third of bursa colorless and apparently only weakly sclerotized; in lateral view (Fig. 18 E), roof of bursa gently declining in distal third; thick tube arising disto-ventrad and proceeding ventro-caudad to first bend, proximal bends about two-thirds the length of bursa, each with a large bladder-like dilation. COLORATION (one female noted below is of a peculiar coloration and is not included in this description): ground color light to *dark brown, never blackish, usually with much yellow. Head with narrow to broad yellow post-ocular stripes (moderate in holotype). Pronotum dorso-medially brown, median carina lighter; dorso-lateral yellow stripes broad and always extending to caudal margin; lateral lobes with dorso-longitudinal black band extending to caudal and cephalic margins, slightly narrower on prozona, usually slightly lighter but broader on metazona (in lightest specimen band is narrower there), no cephalic diagonal or caudad horizontal yellow lines in black band (cephalic line complete in one specimen), the band therefore appearing continuous and of more or less even width in most specimens; ventral half of lobes yellow, ventral carina largely black. Abdomen with mid-dorsal yellow stripe always present, but *brownish and not well-defined in dark specimens, lateral yellow and black spots present but variable in intensity (weak in holotype); tip of abdomen concolorous with rest of abdomen, in some females vaguely marked with orange below. Hind femur with pagina yellow in ventral half, *gray, brown or blackish in dorsal half, this dark stripe often weakly defined or *light and inconspicuous; lunae of geniculae black and brown, ventral half of geniculae usually *orange or blue, sometimes light brown; tibia *unicolored orange (Concordia-Santa Lucía), or bicolored, bluish proximad, purple or wine distad (San Ignacio). MEASUREMENTS (in mm): holotype male: length of body, 32.10; length of pronotum, 6.28; length of tegmen, 4.78; length of fore femur, 5.63; length of hind femur, 17.19; maximum width of hind femur, 4.29. Measurements of the series studied are summarized in Figures 19 and 20.

PARATYPES.— Other than the holotype, all adult specimens examined in this study are designated as paratypes. Male and female paratypes are deposited in the University of Michigan Museum of Zoology, the Academy of Natural Sciences of Philadelphia, the United States National Museum, the British Museum (Natural History), and the Instituto de Biología of the Universidad Nacional de México.

GEOGRAPHIC VARIATION.— Specimens from the only two regions from which this species is known differ significantly in color pattern. In the south, near Concordia, individuals possess orange-red legs, weak and poorly defined grayish paginal stripes, and a complete dorso-longitudinal dark bar across the lateral lobes of the pronotum. Fifty miles to the north, specimens taken near San Ignacio possess purplish and often bicolored tibiae, a jet black and well-defined paginal stripe, and a sometimes interrupted pronotal dark bar. It is interesting to note that where *nigrofasciatus*

occurs within a few miles of its close relative, *contilus similis* at San Ignacio, the leg color is different from both this *contilus* as well as from the not far distant *psolus* near Cosalá. On the other hand, the leg color is similar to another relative, *paloviridis*, with which *nigrofasciatus* is sympatric at San Ignacio. However, *paloviridis* has a different ground color and pronotal and femoral color pattern.

INDIVIDUAL VARIATION.— A single female from 3.6 mi NE Santa Lucía, at a higher elevation and different habitat than our other collections, is distinctively different in color and color pattern from other females. Although the bursa and the tibial color are identical to other females, this specimen completely lacks all the dark and light markings characteristic of *nigrofasciatus* as well as the genus. The specimen is badly rotted, but preservation of at least some of the darker markings would have been expected. Instead, only a vague indication of the dark bar on the lateral lobes of the pronotum is visible.

In males, the apex of the ventral lobe of the sheath is variable. In some it is distinctively different (squarely truncate in side view) from *psolus* and *contilus*, but in others it is indistinguishable from them. In Concordia-Santa Lucía specimens there is considerable variation in the paginal stripe which ranges from almost jet black to a grayish wash.

HABITAT, ASSOCIATED SPECIES AND SEASONAL OCCURRENCE.— All but one specimen were collected along the roadside in thin weeds and bushes or in cut-over heavier growth next to thorn forest. It ranges from the edge of the foothills of the Sierra Madre at 400 feet, well into the mountains at 2740 feet along the Mazatlán-Durango Highway. The single exception is the female described above which was found at 4880 feet at 3.6 mi NE Santa Lucía not far east of the next easternmost locality along the same highway. This specimen was found in oak woods (pines were nearby) among acacias and much succulent undergrowth on a rocky slope with an undescribed relative of *Conalcaea*. At three of the other four *nigrofasciatus* localities, *poecilus* was also common. The fourth locality, 8.3 mi SW Santa Lucía, was not carefully searched, but we suspect *poecilus* was also present because it occurs nearby at higher and lower elevations. *Nigrofasciatus* has not been found at higher elevations in the oak and pine forests at

several localities sampled farther east along this road, nor does it occur on the coastal plain which has been intensively investigated to the north and south, and where *poecilus* is abundant. *Nigrofasciatus* also occurs with *poecilus* as well as *paloviridis* in the low foothills of the Sierra Madre at 1.1 mi SW San Ignacio Ferry. Here in the previously cleared area next to the road, there was a good growth of weeds and bushes next to tall but thinned thorn forest. It was the commonest species here, but surprisingly was absent only a few miles to the north across the Río Piaxtla where *contilus similis* was the commonest species along with *poecilus* and *paloviridis* in a similar habitat but one with more trees and bushes. We have investigated the foothills of the Sierra Madre elsewhere only around Cosalá: no *nigrofasciatus* was found at a number of localities investigated between 700 and 1600 feet, although *psolus* was common, and *paloviridis* and *tridens* were also present at some localities.

Our earliest record for this species is 26 July at 11.5 mi NE Concordia. Only a few adults were found here and at nearby localities during intensive collecting. Most of the adults were teneral and several late instar nymphs were found. Our latest record is 28 November at 1.1 mi SE San Ignacio Ferry, when males and females were common, but less so than in August, and no nymphs were found.

DISTRIBUTION.— Known only from localities between Concordia and Santa Lucía, and at San Ignacio, 50 miles to the north, all in Sinaloa.

RECORDS.— Specimens examined: 24 ♂♂, 28 ♀♀, and several juveniles reared to maturity. For localities see Table 19, p. 104.

Barytettix paloviridis[15] n. sp.
Figs. 1 C-D; 2 B-C; 6 Y-CC; 13 A-B; 14 F, N, V; 15 A-D, F-H, L-N, P-Q; 16 C-D; 18 F, L

HOLOTYPE.— ♂, México, Sinaloa, 2.5 mi NW of Bridge in Culiacán [over the Río Culiacán], 29-30 August 1961 (I. J. Cantrall and T. J. Cohn No. 56); University of Michigan Museum of Zoology.

DIAGNOSIS.— This species may be distinguished from all other *Barytettix* by the combination of an elongate aedeagus, an elongate bursa

---

[15]From the Latin, *palus*, pole or stake, + *viridis*, green, in allusion to the long aedeagus and green body color, and to our facetious reference to this species as "green flagpole" in the early stages of this study.

copulatrix and a usually green ground color. The elongate aedeagus is indicated in undissected specimens by a sac-like enlargement of the pallium, as in all members of the Psolus Group (Fig. 15 H). A few brown individuals are found near Guaymas and Altata, and may be distinguished from the three brown species of the Psolus Group by the lack of distinctive pronotal markings (see Table 6, p. 34), and from brown members of the Humphreysii Group by the elongate aedeagus or bursa. Further comparisons are made in Table 6.

Color comparison of all species of the genus may be found in Table 3, p. 25 , and the geographical distribution of tibial color in Sinaloa may be found under *psolus* in Table 11, p. 49 On the basis of color alone, green *paloviridis* is indistinguishable from green *humphreysii* with reddish legs occurring in southern Sonora, brown *paloviridis* is indistinguishable from *humphreysii* in the Guaymas area, and purple-legged *paloviridis* cannot be distinguished from *poecilus* south of Culiacán (see under geographic variation of *paloviridis,* p. 53). *Poecilus* is red-legged as in *paloviridis* but only far south of the range of *paloviridis.* Male *paloviridis* can always be recognized from *humphreysii* and *poecilus* by the enlarged pallium.

Compared with other members of the Psolus Group, *paloviridis* stands apart in color, color pattern, dorsal aedeagal valves, ventral lobes of the aedeagal sheath, disto-dorsal origin of the thick tube of the receptaculum seminis, and more distal position of the distal sclerite of the bursa copulatrix (Table 6). Surprisingly the ventral valves of the aedeagus of *paloviridis* populations south of the area occupied sympatrically with *psolus* are similar to *psolus* in several details (see under the discussion of geographic variation in *paloviridis*). North and south of the area of sympatry, the apices of the ventral aedeagal lobes of *paloviridis* tend to be less compressed and appressed and thus are similar to the general condition found in *psolus* (Figs. 15 M-O). The dorsal valves of *paloviridis* are more similar in general shape to *nigrofasciatus* (Figs. 14 F, H; 15 A-E), and northern and southern colonies possess a median hump on the valves somewhat as in that species (Figs. 15 C, E). *Paloviridis, psolus* and *nigrofasciatus* all have similarly elongate aedeagi, bursae, and proximal bends of the thick tube, similar dilations of the thick tube, and a generally similar, almost invisible phallo-

treme, in contrast to the conditions in *contilus.* Comparisons are summarized in Table 6, and phylogenetic implications will be discussed in a later section dealing with the relationships of all *Barytettix.*

SPECIES DESCRIPTION (in variable characters, condition in holotype is indicated by asterisk preceding that condition).– CERCUS (Figs. 6 Y-CC): dorsal margin *almost straight to weakly concave; disto-dorsal portion not at all to slightly enlarged (but entire cercus may be very broad); disto-ventral tooth weakly to *moderately produced, acute. AEDEAGUS (Figs. 1 C-D, 13 A-B): elongate (0.19-0.38 times length of pronotum, 0.29 in holotype), and narrow (length 2.2-2.9 times mid-dorsal width, 2.6 in holotype). DORSAL VALVES: in cephalic view (Figs. 14 F; 15 F-G, P-Q), convex dorsally but flaring laterally for proximal two-thirds, becoming more or less flat distad, medial margins of free lobes diverging only slightly distad, forming a narrow V, lateral margins weakly convex, valves tapering to short (Guaymas colonies) or *long, rounded apices which lie along medial margins of dorsal surface of ventral valves; fused portion usually with two low, longitudinal ridges (barely indicated in holotype), ending in one or two humps distad (northern and southern populations), or *without humps (middle populations); in lateral view (Figs. 13 A, 15 A-D), ventral margin convex or sinuate (Guaymas colonies), or more or less straight or *weakly sinuate, usually exposing ventral valve for most of its length. VENTRAL VALVES: in cephalic view (Figs. 14 F, 15 P-Q), *almost completely obscured by dorsal valves, or lenthily exposed, visible surface *more or less flat, or sloping laterad, or weakly convex, lateral walls of phallotreme *invisible (middle colonies, Fig. 15 P), or barely visible apically where walls flare slightly (Fig. 15 Q); in lateral view (Figs. 13 A, 15 A-D), latero-ventral margin straight (Fig. 13 A), weakly convex (Fig. 15 A) or *with distal third gently curved (middle colonies) (Fig. 15 D), sometimes *with a strong median convexity (Figs. 15 B, D), usually completely exposed by dorsal valve, distal quarter *uniformly thin (middle colonies), or distal sixth tapering rapidly to apex (compare Figs. 15 D and 13 A); in caudal view (Figs. 13 B, 14 N, 15 F-G), touching to or beyond middle, then medial margins diverging usually more strongly than in *psolus,* but becoming parallel distad, often *slightly convergent near apices, or divergent to apices (Guaymas colonies), lateral margins more or less straight and parallel (Guaymas and Guamúchil colonies, Figs. 15 F-G), or *parallel in proximal half, weakly emarginate near middle, and weakly convex or *sinuate in distal half (Figs. 13 B, 14 N), rarely distinctly emarginate in distal half, ventral surface with distal half or third convex and appearing half twisted outward (Guaymas and Guamúchil colonies), or *more or less flat and broad (middle colonies, Fig. 14 N) or somewhat flat, narrow, twisted slightly inward and often slightly concave (southern colonies, Fig. 13 B), proximal half or two-thirds of surface *more or less flat, or weakly or moderately concave longitudinally, often with a *lateral swelling near middle which is sometimes *prominent (Fig. 14 N) and sometimes continued to base as a ridge. RAMUS OF CINGULUM (Figs. 1 C-D): ventro-distal portion narrow, ending considerably proximad of junction of dorsal valves with ventral lobes of sheath, thus exposing a lengthy portion of ventral lobes. VENTRAL LOBES OF SHEATH (Figs. 13 A-B; 15 A-D): lengthily developed proximad of junction of dorsal valves and partly sclerotized there, proximal portion strongly but briefly reflexed or flanged (greatly elongated distad of junction into two approximate, finger-like structures which usually project along their entire length at a variable angle from ventral valves (appressed to valves only in Guamúchil samples); in lateral view (Figs. 13 A, 15 A-D), dorsal margin usually straight, rarely *weakly convex (Fig. 15 D), apices usually roundly truncate, disto-dorsal angle usually relatively sharp, disto-ventral angle usually rounded, ventro-proximal portion weakly enlarged, *straight or weakly arcuate below,

provided with an elongate sclerite (process of ramus of cingulum) on either side; in distal view (Figs. 15 L-N), apices usually somewhat to strongly compressed (moderately compressed in holotype), parallel, often appressed, rarely round (apices meeting at a broad angle only in Guamúchil colonies, Fig. 15 L, but lengthily flat, unlike *contilus* and its relatives), proximal enlargement variable, often *keel-shaped, often somewhat rounded (flat only in Guamúchil colonies). BURSA COPULATRIX AND THICK TUBE (Figs. 2 B-C; 15 C; 18 F, L): bursa elongate (length 3.0 times width), strongly sclerotized; in cross section (Fig. 18 L), concave dorsally, convex ventrally; sclerotization divided into proximal and distal sclerites by a colorless flexible area, proximal sclerite strongly pleated dorso-laterally and appearing weak and colorless along mid-line, distal sclerite proximally uncolored but pleated, distal portion pigmented, extending across bursa, truncate or notched distally, distal fifth of bursa only weakly sclerotized; in lateral view (Fig. 18 F), roof of bursa more or less concave in distal third; thick tube arising disto-dorsad, gently recurved and proceeding ventro-caudad to first bend, proximal bends about two-thirds the length of bursa, each with a very large bladder-like dilation. COLORATION: ground color green, abdomen and caudal femur often yellowish (ground color brown only in individuals from Guaymas region and Altata). Head with yellow post-ocular stripes *sub-obsolete or missing. Pronotum sometimes with a *dorsal, narrow, dark, median stripe on pro- and mesozona; dorso-lateral yellow stripe narrow and restricted to pro- and mesozona (broad and extending to caudal margin only in some individuals near Guaymas), sometimes absent (probably resulting from poor preservation); black spot of lateral lobes restricted to pro- and mesozona (extending briefly onto metazona and continued as a dark wash to caudal margin only in some individuals near Guaymas), spot usually completely divided by cephalic diagonal yellow line (barely capped by black in holotype), caudal horizontal yellow line in spot often *incomplete, sometimes absent, spot narrowly bordered ventrad by yellow, ventral quarter and ventral carina green (ventral surface of carina black in a few individuals in Guaymas colonies). Abdomen always with *well-defined mid-dorsal yellow stripe, but sometimes obsolete on metanotum and first abdominal segment; dorso-lateral yellow and black spots usually present, yellow spots often obscured apparently by poor preservation; supra-anal plate, cerci, and dorsum of subgenital plate usually *reddish (purplish in individuals with purple tibiae), probably always so in life, but fading in poorly preserved specimens (in Guaymas colonies, tip of abdomen yellowish or with weak trace of red in green individuals, or light brown in brown individuals). Hind femur with pagina *green to yellow, *unicolorous, or with a variously developed green or brown dorsal stripe, darkest in southern colonies; carinae *dark green to black; geniculae reddish (purplish in individuals with purple tibiae) or in Guaymas colonies, yellowish brown, lunae *black or brown. Caudal tibia dull *red-wine over most of range, purplish in some southern individuals, *unicolored, or weakly and inconspicuously bicolored. MEASUREMENTS (in mm): holotype male: length of body, 31.76; length of pronotum, 6.55; length of tegmen, 5.55; length of fore femur, 5.79; length of hind femur, 16.63; maximum width of hind femur, 4.54. Measurements of the series studied are summarized in Figures 19 and 20.

PARATYPES.— All adult specimens examined in this study except the holotype, are designated as paratypes. Male and female paratypes are deposited in the University of Michigan Museum of Zoology, the Academy of Natural Sciences of Philadelphia, the United States National Museum, the British Museum (Natural History), and the Instituto de Biología, Universidad Nacional de México.

GEOGRAPHIC VARIATION.—*Paloviridis* displays considerable geographic variation, a situation not unexpected in view of its extensive range through arid and subhumid habitats and its sympatry with several other species of *Barytettix*. The extreme northern populations around Guaymas, and those west of Guamúchil in the middle of the range, each show distinctive features sharply different from the other populations of the species. The significance of these variants is unknown, although each of these populations occupies a habitat somewhat different from the rest of the species. In the more southerly populations, several variant characteristics are found which resemble nearby or sympatric populations of the distantly related *poecilus*. Finally, and of particular interest, the pattern of variation in certain other characters over the whole range of the species strongly suggests reproductive interaction with closely related species. This pattern has been used as evidence of mechanical reproductive isolation (Cantrall and Cohn, 1972). Each of these four situations is discussed in detail below.

The Guaymas Populations and Dwarfism.— The northernmost colonies of *paloviridis* (18 mi N and 8 to 21 mi SE Guaymas) are characterized by their small size, dull green or brown ground color, and by distinctive ventral aedeagal valves. These are thick and short, with acute apices, parallel lateral margins, evenly divergent inner margins, and strongly tilted, convex ventral surfaces of the distal halves of the valves (Figs. 15 A-B). This construction is somewhat similar only to the *paloviridis* west of Guamúchil and near Altata, both localities far to the south. However, those individuals have longer, more slender and thinner valves with sinuate lateral margins (Figs. 15 C, F, G). In other aedeagal characters, the Guaymas colonies generally match those of adjacent colonies, whereas the Altata and Guamúchil colonies are similar to southern *paloviridis*, or possess their own unique features (Guamúchil ventral lobes, see below).

The Guaymas colonies, sampled in three different years, average smaller than all other *paloviridis*, and include the smallest individuals in the species (Table 12). Only the colony at Altata, far to the south, approaches the size conditions of the Guaymas populations. Most other samples do not overlap the Guaymas range and average well over 6 mm in pronotal length. Inter-

TABLE 12

DWARF SIZE POPULATIONS IN *BARYTETTIX PALOVIRIDIS*

Locality and date of collection	Number of specimens	Male pronotal length (mm)	
		Range	Mean
Guaymas (1966, 1968, 1970)	22	4.2-6.0	5.1
40 mi S Navajoa (160 mi SE Guaymas) (1968)	6	5.1-6.2	5.8
12.2 mi N Los Mochis (206 mi SE Guaymas) (1968)	7	5.1-6.0	5.4
10.9 mi W Guamúchil (272 mi SE Guaymas) (1968)	16	5.5-6.5	5.9
Altata — 15 mi SW Navolato (350 mi SE Guaymas) (1968)	15	4.8-5.5	5.4

estingly, the few other colonies which do overlap the range, and average below 6 mm, are also the geographically closest ones (Navojoa-Guamúchil) (see Table 19, p. 104). All of these were collected in 1968. In other samples collected near the Navojoa, Los Mochis and Guamúchil localities in preceding years, the minimum and average sizes are much larger, thus indicating size variation from year to year.

The dull green color of the Guaymas individuals is found nowhere else within the range of the species, and the brownish individuals are similar only to some members of the Altata colony. In the two darkest brown Guaymas individuals, the black spot of the lateral pronotal lobes extends as a dark wash to the caudal margin of the pronotum. They also possess a very narrow black line on the ventral surface of the ventral carina of the lateral lobes. These color characteristics seem to be a development toward, or a reduction from the condition in *psolus* and its brown relatives, but there are no other similarities to those species in color or aedeagal structures.

The size and color of the Guaymas populations are matched by the nearby *humphreysii* colony at 22.7 mi SE Guaymas. This leads us to suspect that small size and brown or dull green color are responses to environmental conditions of a flat area almost at sea level where the soil is probably saline. The only other collections of *Barytettix* made at this elevation have been among the dunes near Altata where *paloviridis* is again small and often brown. Although the flats near Guaymas seem very different from the dunes at Altata, there are probably several environmental factors common to the two areas which are different from nearby higher and often hilly localities where both species are larger and greener. It should be noted, however, that the northernmost of the Guaymas colonies (18 mi N Guaymas) is located inland and at a somewhat higher elevation, but possesses the same characteristics as those on the coast (except for brown individuals), whereas in a nearby *humphreysii* colony found just behind the beach sand 4 mi W Guaymas, all individuals are large and bright blue-green.

The Guamúchil Populations and Primitive Aedeagal Characters. — The two colonies of *paloviridis* found west of Guamúchil possess distinctive ventral lobes of the aedeagal sheath. When seen in distal view, the valves usually form an open V (Fig. 15 L) in contrast to the parallel and often appressed lobes in all other colonies of this species (Figs. 15 M-N). This feature is somewhat variable in our material: in 15 individuals, the lobes form an open V as described and figured; in four, the lobes form a much narrower V (one of them closely resembling the condition in

nigrofasciatus, Fig. 15 K); and in one individual, the lobes are fully as twisted toward one another as in the rest of the species. This last individual has the apices of the lobes rounded in distal view, a relatively uncommon condition in *paloviridis*. In the nearest *paloviridis* colony to the south, 5 mi SE Guamúchil, one male out of the six collected shows a strong tendency to the open V condition, and a second has a narrower V condition. Several males in this colony also have the apices rounded. There is a similar but weaker tendency toward the Guamúchil condition in the next northern colony at 12.2 mi N Los Mochis.

The ventral lobes lie flat against the ventral valves in most of the Guamúchil specimens. In this position they strongly resemble the ventral lobes in *humphreysii* (compare Fig. 15 G with Figs. 9 B and D), and thus may represent the ancestral condition in the Psolus Group. However, the lobes in the Guamúchil colonies are already more elongate than in *humphreysii* and when they project away from the ventral valves they do so along their entire length as is typical in the Psolus Group, rather than briefly or only at the tip as in *humphreysii*.

The Guamúchil colonies also possess what at first glance appears to be unusual ventral valves. They are narrow and have diverging inner margins, acute apices, and strongly convex ventro-distal surfaces (Figs. 15 F-G). However, this type of valve is almost identical to that in the Altata colonies 80 miles to the south, which differ only in having the valves slightly less acute and less divergent. Nor are the Guamúchil valves very different from those in the next northern colonies (between Los Mochis and Navojoa) where they are somewhat wider, less acute, slightly incurved, and sometimes flatter ventrally. Still farther north, the Guaymas populations display such features of the Guamúchil type as the diverging inner margins, convex ventro-distal surface, and acute apices, but the valves there are much thicker, shorter (Figs. 15 A-B), more divergent, and have straight rather than sinuate lateral margins. Thus the Guamúchil valves are markedly different only from the very broad, blunt, incurved and ventrally flat valves possessed by the populations north of Culiacán (Figs. 14 F, N; 15 D). Even in this case, the geographically intermediate colony at 5 mi SE Guamúchil (62 mi NW Culiacán) is intermediate in valve morphology. Southeast of Culiacán, the valves are again

somewhat similar to those at Guamúchil (Figs. 13 A-B). There may thus be an irregular north-south cline in valve characteristics interrupted by the strikingly different valves in the middle between Guamúchil and Culiacán. There is good evidence that the unusual type found between those two cities is a response to special circumstances in that region, a topic which will be discussed below.

It is tempting to speculate on the possibility that the Guamúchil colonies have retained several of the more primitive aedeagal features of the species. Under this hypothesis it is difficult to explain why the populations to the north and south both possess the same derivative conditions. Possibly the Guamúchil colonies represent a recent intrusion of a more eastern, foothill population. Much more collecting needs to be done east of the main highway as well as along the coast in this region before the problem can be adequately explored.

In view of the mosaic of aedeagal similarities and intermediates, we do not think that any purpose would be served in designating the Guamúchil population as a subspecies.

Leg Color and Interaction with Poecilus.— Certain color characteristics of southern populations of *paloviridis* are of interest because of their resemblence to the unrelated *poecilus* which occurs in the same region. All *paloviridis* populations between Culiacán and Mazatlán possess tibiae which are distinctly but slightly more purple than those in the north. Most individuals have wine-red tibiae, but purple tibiae are found as individual variants in several populations from 37 to 60 mi SE Culiacán, north of the range of *poecilus*. The purple of these individuals is indistinguishable from the purple found uniformly in all northern populations of *poecilus*. However, in the zone of the overlap of the two species between 66 mi SE Culiacán and 20 mi N Mazatlán, all *paloviridis* individuals possess reddish or wine-colored tibiae. On the other hand, it is in this general area that *paloviridis* possesses a dark paginal stripe on the hind femur as is found in all northern colonies of *poecilus*. The presence of the stripe is variable and it is usually weak in colonies of *paloviridis* between Culiacán and 30 mi SE Culiacán, but in all colonies farther south it is always present and is as dark as in *poecilus*. This pattern of geographic variation may also be the result of interaction with *psolus* and *contilus* (see discussion below). Thus, there

are *paloviridis* individuals very close to the zone
of sympatry with *poecilus* which are indistin-
guishable from the latter species in external ap-
pearance. No evidence of interbreeding has been
found in the genitalic characters of these popula-
tions, thus eliminating the possibility of the ori-
gin of these *poecilus* characteristics in *paloviridis*
through introgression. The tibial color differ-
ences in the sympatric populations may be a case
of character divergence resulting from copulation
errors, even in the absence of hybridization.
However, initial cage studies suggest that males
do not differentiate between differently colored
females. Furthermore, the colonies between
Navojoa and Los Mochis also have wine or pur-
plish tibiae in an area of overlap with similarly
colored, green *humphreysii*. North and south of
this area *paloviridis* usually has redder tibiae.
This problem is discussed further in the section
on Promising Problems.

*Aedeagal Character Reinforcement and Me-
chanical Reproductive Isolation.*— The pattern
of geographic variation of most biological signifi-
cance is that of the marked shift in the variation
of many characters at the Río Culiacán and Río
San Lorenzo. This is coupled in a few of the
same characters with a similarity of populations
south of Culiacán with those northwest of
Guamúchil but separated by distinctive popula-
tions in between. This pattern of variation en-
compasses all geographically variable characters
studied with the exception of features unique to
the Guaymas and Guamúchil colonies, and tibial
color.

The geographic variation in eight aedeagal
characters over the whole range of the species is
illustrated in Figures 3 and 4, which should be
used in conjunction with the analysis presented
below. The localities in Figure 3 have been ar-
ranged from northwest to southeast following
the main west coast highway along which most
of the collections have been made. In Figure 4
we have grouped localities to the east and west
of the main highway in the vicinity of Culiacán,
and have repeated the histograms for localities
immediately north and south of Culiacán. These
eastern and western populations vary somewhat
from the above pattern and are discussed sepa-
rately. To shorten both figures, some samples
have been grouped where differences between
them seemed minimal. No attempt has been
made to make the grouped samples equivalent
or equidistant. In most of the qualitative char-

acters the intermediate conditions were subjec-
tively determined and should not be considered
definitive. Bars have been blackened to empha-
size the pattern. Where a histogram includes
three conditions, the leftmost bar has been
blackened; if there were four or five conditions
graphed, the leftmost two bars were blackened.

Parenthetically it should be noted that the
Guaymas and Guamúchil populations closely
follow the pattern of adjacent ones in at least
five of the eight characters graphed. This sug-
gests that they have not been isolated from the
rest of the species and thus are not worthy of
subspecific designation.

Every character illustrated in Figure 3 shows
a marked shift in variation at the Río Culiacán
or within six miles south of it. This shift often
occurs over a distance of 3.5 miles in large col-
lections on either side of the river and as close
to it as the habitat permits. The condition in
two of the characters (length of exposed ventral
valve and depth of apex of ventral valve) south
of the Río Culiacán, and particularly south of
the Río San Lorenzo is similar to that northwest
of Guamúchil. Two other characters (dorsal
valve hump, and ventral valve width) show the
same pattern of similarity, except for the differ-
ent Guaymas populations. Between 23.9 and 30
mi SE Culiacán, there is a clear reversion in all
but two characters (dorsal valve hump, ventral
valve width) to the condition of the colonies
north of Culiacán. These six characters shift
even more sharply across the Río San Lorenzo
in a distance of less than three miles.

It is precisely in the region between Culiacán
and Guamúchil that the closely related *psolus*
occurs and is sharply limited to the south by the
Río Culiacán (it is present south of the river only
at the south end of the railroad bridge where it
may be a recent arrival). Between 23.9 and 30
mi SE Culiacán another related species, *contilus
dicranatus,* is found. Both *psolus* and *c. dicrana-
tus* occur commonly in the same general habitat
with *paloviridis,* and are sometimes found roost-
ing at night in the same bush with *paloviridis.*
We thus suspect that the distinctive *paloviridis*
characteristics in these areas of sympatry and the
sharp shift in variation immediately beyond them
are the result of interaction of *paloviridis* with
its congeners.

In the area of sympatry, the condition of all
but two of the characters (dorsal valve hump,
and width of ventral valves) in *paloviridis* is very
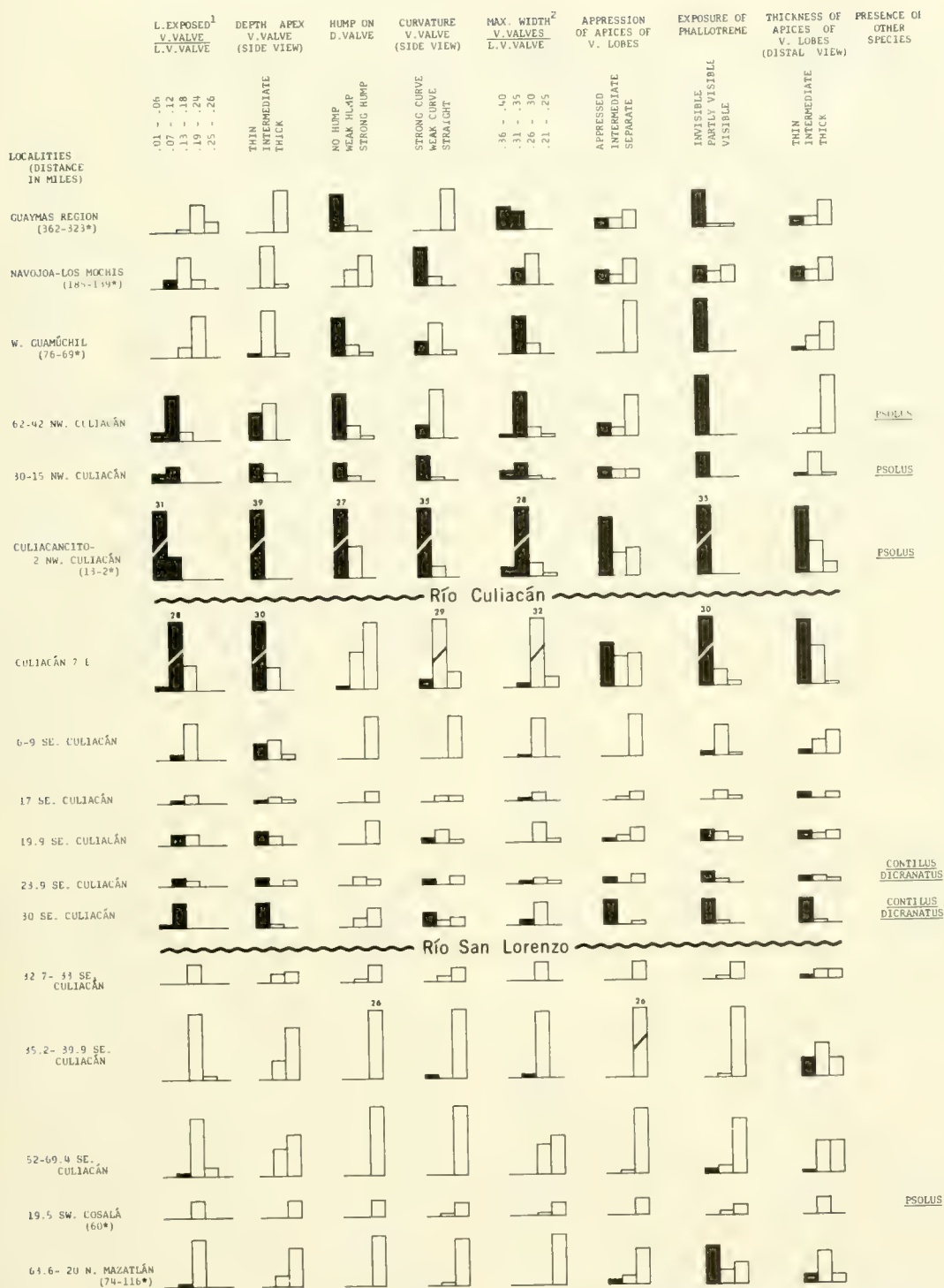
Figure 3. Aedeagal variation in *Barytettix paloviridis* throughout its range. Bars have been blackened only to emphasize the pattern: the black bars generally represent conditions of the populations immediately north of Culiacán, and the white bars, conditions found south of Culiacán. In histograms with three conditions, only the left bar has been blackened; in histograms with four or five conditions, the left two bars have been blackened.

*miles from Culiacán
[1] the greater the ratio, the more valve is exposed (Fig. 15 Q in contrast to Fig. 15 P)
[2] The greater the ratio the wider the valves
Scale: height of bar represents numbers of specimens measured or scored. The lowest bar represents one specimen, the highest unbroken bar, 25. A number over a broken bar indicates numbers over 25.

different from *psolus* and *c. dicranatus,* whereas to the south and often to the north of that area the *paloviridis* conditions are similar to those of the other two species (Figs. 15 P-R). The degree of exposure of the ventral valves and of the phallotreme can be seen to be directly associated with the difference between *paloviridis* females and *psolus* and *c. dicranatus* females in the position of the aperture of the thick tube of the receptaculum seminis (Figs. 18 B, H, D, J, F, L). The aedeagal condition of *paloviridis* where it is sympatric with those species would interfere with the entry of the spermatophore tube into the more ventral opening of the thick tube of either *psolus* or *c. dicranatus.* The function of the other aedeagal structures is not so obvious, but each could well be associated with the proper seating of the aedeagus in the bursa of the female. Thus conditions in the *paloviridis* aedeagus which are different from those of *psolus* or *contilus* might prevent its proper seating in the bursa of those species and thus prevent insemination. The function of these aedeagal structures and their role in interspecific crosses are discussed in greater detail in the section on Mechanical Isolation.

A ninth character which we have not included in Figure 3 because of difficulty in precision of analysis is the sculpturing of the ventral surface of the ventral valves. This character appears to follow the same pattern described above, at least southeast of Guamúchil. In the area of sympatry with *psolus* and *c. dicranatus* the valve surface is relatively smooth and more or less flat from side to side, but south of this area it is excavate distad and longitudinally ridged mesad as in *psolus* (see under Species Description). There seems to be an area of transition and variability south of Culiacán, but in the southern end of the range of the species the valves in ventral view are generally similar to those of *psolus* (except for their only slightly sinuate lateral margins and the strong mesal and proximal excavation of the ventral surface). It is difficult to envision a function for such sculpturing or the lack thereof. A detailed study of the interior surface of the female bursa may reveal such a function. Northwest of Guamúchil, and near Altata, the ventral surface of the valve is usually convex, a condition not found in any of the more southerly populations.

There exist several apparent exceptions to this pattern of variation and similarity which might

be used to test our hypothesis of reinforcement of aedeagal characters in response to the presence of closely related species. One exception to the pattern of a strong shift in variation at the Río Culiacán can be seen in the characteristics of the populations east of the Río Humaya, illustrated in Figure 4. These populations lie to the east of the main northwest-southeast transect, and their variation can be compared in the figure with that in nearby or adjacent populations in the main transect.

The east side Río Humaya populations (NE Culiacán) agree closely with those on the west side (NW Culiacán) in six characters, all of which show a strong shift at the Río Culiacán, but they are more similar to populations southeast of Culiacán in two others, the dorsal valve hump and the ventral valve width. These are the same two characters which fail to change between 23.9 and 30 mi SE Culiacán where other characters revert to conditions found northwest of Culiacán (Fig. 3). Thus the colonies east of the Humaya are almost identical in all features to those at 23.9-30 mi SE Culiacán. It is precisely in these two areas that restricted colonies of the related species *contilus* are found, *c. dicranatus* in the southern area and the nominate subspecies east of the Humaya. Thus, the difference in the characteristics of the *paloviridis* colonies on either side of the Humaya is probably the result of a different response to the presence of *psolus* than to the presence of *contilus.* However, *psolus* is also found on the east side of the Humaya, south of Tepuche. It is unfortunate that our samples are too small to determine reliably whether *paloviridis* south of Tepuche and sympatric with *psolus* is different from samples north of Tepuche where it is sympatric with *contilus.* The trend in variation is in the expected direction in each area. However, the ventral valve width in the south Tepuche sample (sympatric with *psolus*) is even more different from northwest Culiacán *paloviridis* also sympatric with *psolus,* than from the north Tepuche sample allopatric to *psolus.* It is possible that all *paloviridis* populations east of the Humaya are more strongly influenced by gene flow from those south of the Río Culiacán. The eastern extension of the Río Culiacán — the Río Sanalona — is smaller, and there is much less intensive agriculture east of the city. In contrast, the northwest Culiacán populations are separated from those south of the Río Culiacán by the
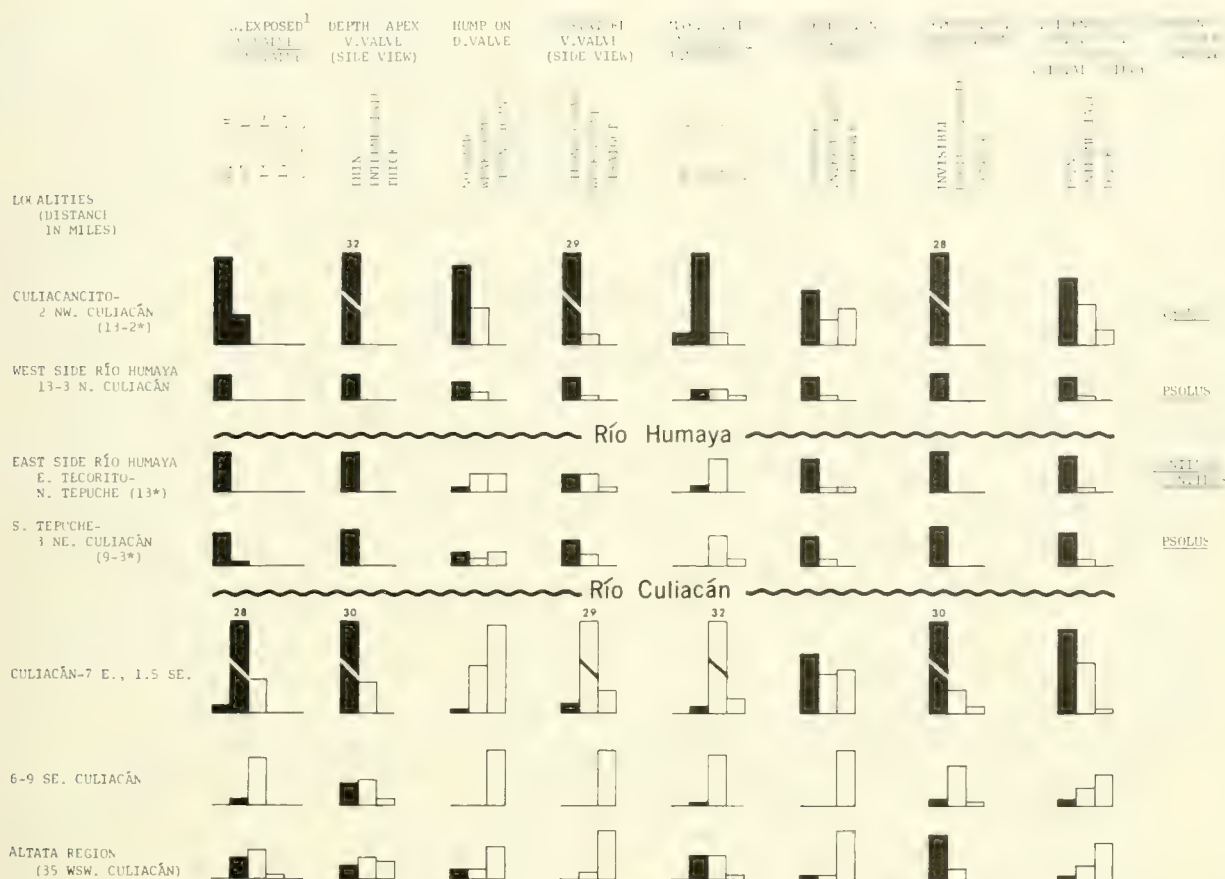
Figure 4. Aedeagal variation in *Barytettix paloviridis* in the Culiacán region of Sinaloa. For explanation see legend for Fig. 3, p. 57.

larger river, the city itself, and the intensively farmed, irrigated land to the west and southwest. It is also possible that *psolus* may have only recently arrived on the east side of the Humaya (as suggested by Cohn, 1965, for the katydid *Neobarrettia hakippah*) or that it is present there in small numbers.

Another apparent exception to the general pattern is the lack of change in those southern *paloviridis* populations which are in contact with other *contilus* subspecies, *tectatus, hiscatus* and *similis* (at 7-9, 19.9, and 66-74 mi SE Culiacán respectively) or with southernmost *psolus* (at 19.5 mi SW Cosalá) (Fig. 3). This seems to contradict our hypothesis of the cause of the marked shift in the characteristics of *paloviridis* where it is sympatric with *c. dicranatus* or with *psolus*. However, the bursae of *similis* and *tectatus* (Figs. 18 A, G, C, I) are somewhat different from that of *dicranatus* (almost identical to Figs. 18 B, H) in the position of the aperture of the thick tube, and it seems reasonable that neither of these two could be inseminated by any *palovi-*

ridis. This point is further discussed in the section on Mechanical Isolation. As for *hiscatus,* that subspecies appears to be rare, at least along the main highway where we have done all of our sampling within its apparent range. The area was specifically searched for *hiscatus* in 1970 by Cohn who found abundant *paloviridis* but only one questionable female *hiscatus*. It is possible that any influence of *hiscatus* on *paloviridis* is swamped in this area. The effect of the nominate subspecies on *paloviridis* is almost exactly the same as that of *dicranatus* and has been discussed above.

We have no such easy interpretation for the lack of change in *paloviridis* where it is sympatric with the southernmost colony of *psolus*. The ranges of the two may not overlap much beyond the point where they were found together at 19.5 mi SW Cosalá. The road was sampled at several points between that locality and 5.6 mi NE Cosalá at higher elevations. *Psolus* was generally common and *paloviridis* absent. On the other hand, *paloviridis* was abundant and *psolus*

absent at lower elevations along the main high-way only about 10 miles to the west, where the highway has been intensively worked for many miles to the north and south. Thus any ten-dency toward a change in characteristics in the sympatric *paloviridis* populations may be quickly swamped. It is also possible that one or the other species has only recently arrived in the area, for it is near or at the edge of the range of both. That there is selective pressure for diver-gence of one from the other at this locality is indicated by our observation here of one of the few cases of interspecific copulation (♂ *psolus* X ♀ *paloviridis*).

The marked shift in the southernmost *palovi-ridis* population toward a closed phallotreme is puzzling, but may be the result of interaction with nearby *nigrofasciatus*, the bursa of which is very similar to that of *psolus.*

Another exception is seen in the Altata popu-lation (Fig. 4) which is found just behind the coast west-southwest of Culiacán, but north of the Río Culicán. Despite its geographic position this population is similar to those southeast of Culiacán in four characters (depth and curvature of ventral valves, appression and thickness of ventral lobes), shows strong southeast influence in three characters (exposure of ventral valves, dorsal valve hump, ventral valve width) and is similar to the northwest Culiacán populations in only one character (phallotreme). The region is clearly deltaic and is drained by many streams. The Río Culiacán flows west of Culiacán to Nav-olato where it makes a sharp bend to the south and empties to the sea well south of Altata. It is interesting to note that another river which drains the Navolato area flows northwest to enter the sea north of Altata. This is called the Río Viejo, and we suspect that this may have been an older drainage channel for the Río Cul-iacán. Therefore, it is likely that the Altata pop-ulation may have been in freer contact with southern colonies in the recent past. Further-more, *psolus* has not been found in the area (but it has not been searched carefully), and there may thus be little selective pressure for the main-tenance of northwest Culiacán characteristics. In the one character displaying the strongest northern influence (exposure of the phallotreme) there is more variation in the Altata population than is found in any of the Culiacán-Guamúchil colonies.

Two final exceptions are more difficult to interpret. The pattern of similarity where *palo-viridis* and *psolus* are allopatric and of difference where they are sympatric is reversed in two char-acters. The dorsal valve hump is absent and the width of the ventral valve is greater where the species are sympatric. Although it is not at all clear to us why these two features should be similar to the condition found in *psolus,* the change occurs concomitantly with the change in the other six features of the aedeagus at the Río Culiacán. It seems certain that the morphology of the aedeagus has much to do with the proper placement of the spermatophore tube. Our pres-ent lack of information regarding the function of the hump and the relative width of the ventral valves, as they relate to the bursa copulatrix, prevents an explanation as to how the shape of these two features can contribute to mechanical isolation. We anticipate that a study of the re-lationship of the male and female copulatory structures in interspecific mating pairs will go far in elucidating this problem. Presently, we do know that the ventral valves are shaped quite differently where the two species are sympatric although the measurements of width are similar. In *psolus* the widest part of the valves is at the distal quarter, with the narrowest portion imme-diately proximad, whereas in *paloviridis* the widest portion is at the distal third or more proximad, and the valves narrow more gradually proximad. This difference may create a differ-ence in the seating of the aedeagus in the bursa.

A non-genitalic character which seems to fol-low the same pattern of variation and similarity is femoral color. This character has not been in-cluded in the figures because of difficulty in pre-cisely differentiating the conditions. South of the Río San Lorenzo (32 mi SE Culiacán, see Fig. 3), all *paloviridis* possess a well-marked dark paginal stripe of dark green, brownish or gray-black. As in the genitalic characters there is a very sharp break across the Río San Lorenzo; all specimens immediately south of the river (32.5-33 mi SE Culiacán) have a dark stripe, while all specimens immediately north of the river (30-23.9 mi SE Culiacán) in the range of *contilus dicranatus* lack the stripe. Farther north, in the range of *psolus*, occasional *paloviridis* specimens have a well-marked stripe, some have a weak stripe, but most have none at all. Both *contilus* and *psolus* always have a sharply defined black paginal stripe. In *paloviridis*, the absence of such

a stripe north of the Río San Lorenzo and its presence south of that river might be another instance of character reinforcement similar to that in genitalia discussed above, although our preliminary findings suggest that some species of *Barytettix,* at least, do not depend on color or color pattern to identify their mates. As in the genitalic pattern, there is no reinforcement in paginal striping where *paloviridis* is sympatric with *contilus similis* at 66 and 74 mi SE Culiacán, or at 19.5 mi SW Cosalá where it is sympatric with *psolus.*

The Barrier Effect of Rivers.— These data on variation in aedeagal and femoral color characteristics also demonstrate how effectively rivers act as barriers to the distribution of *Barytettix* species. We have hypothesized above that the conditions at 30 mi SE Culiacán in six of the eight characters graphed in Figure 3 are the result of interaction with *c. dicranatus.* That subspecies has not been found south of the Río San Lorenzo, where each of the six characters shows a marked shift in condition. Not only does the colony on the south bank (32.7-33 mi SE Culiacán) possess the alternative condition in each to those on the north bank, but the characters are not even more variable than in the colonies to the south. There seems to be minimal gene flow across this river. This is not true in the *paloviridis* colonies north of the northernmost *dicranatus* at 23.9 mi SE Culiacán. No river intervenes between the *paloviridis* colony at that locality and others farther north. Nor has *dicranatus* ever been found north of that point despite intensive survey work in the area. The influence of *dicranatus* can be seen extending at least four and possibly as far as 6.9 miles to the north. In one character (exposure of ventral valves) a remarkably smooth cline is shown, despite the inadequacy of the sample sizes. It is possible that swamping might be more effective in the south because the populations there are of larger extent. The nearest *psolus* is only about 24 miles north of the *dicranatus* colony, and may thus have some influence on populations south of Culiacán. This is suggested by the variability of *paloviridis* in the city itself just south of the river. However, at 6-9 mi S Culiacán, at least four of the characters are uniformly different from those in the colonies sympatric with either *psolus* or *dicranatus.* In each of these there is a cline southward.

A similar shift in seven of the eight characters occurs at the Río Culiacán west of the Río Humaya, over a distance of at most 3.5 miles (Fig. 4). In this case the variation is greater, suggesting greater gene flow. This variation may be the result of the presence of *psolus* on the south bank of the river at one locality, where we suspect it is a recent arrival.

HABITAT AND ASSOCIATED SPECIES.— *Paloviridis* appears to occupy a somewhat different habitat north of Los Mochis than south of that city. In the north, the coastal plain vegetation is largely desert or thorn scrub, and here *paloviridis* is found only in areas of denser vegetation usually along water courses. It occurs in the weedy and bushy edge of these habitats which resemble thorn forest but which are usually lower and more open. Where it is found in the vicinity of Guaymas, *paloviridis* is the only *Barytettix* present although the widespread and common *humphreysii* is found in numbers in both more open and more densely vegetated habitats nearby. The two species are found together only at Estación Luis, 40 mi SE Navojoa, at the edge of what appears to be a patch of thorn forest. To the south, *paloviridis* is again found alone at 12.2 mi N Los Mochis in a densely bushy arroyo. This locality is well within the range of *tridens* which occurs, like its close relative *humphreysii,* in more open and more dense vegetation to the north and south of the *paloviridis* locality. The exclusive occurrence of *paloviridis* in regions where *humphreysii* or *tridens* are common and widespread is puzzling and suggests some kind of interaction between them or special habitat requirements of each.

South of Los Mochis, *paloviridis* is abundant in almost all weedy bushy ruderal habitats, in weedy or overgrown fields, and at the edge of thorn forest. In the more open and disturbed habitats, especially along the main highway, it is almost continuously distributed and is often the only *Barytettix* species present. It is absent from the most intensively cultivated areas near Los Mochis, possibly because even the roadsides had once been scraped clear, or because of extensive spraying.

Although *paloviridis* has been found within thorn forest (but always near the edge) as at 3.1 mi N Tepuche, some of our data suggest that this species is poorly adapted to that habitat, or is at a disadvantage there relative to its congeners.

First, it was conspicuously absent from the thorn forest at two localities where other *Barytettix* species were common (5.3 mi NW Badiraguato and 6 mi W Jesús María). Second, at 51.7 mi SE Culiacán, it was abundant in a bushy area adjacent to thorn forest, but absent from the thorn forest itself, where *tridens* was moderately common. Finally, it was absent from the open weedy summit of Cerro Tule, 7 mi SE Culiacán, where *contilus tectatus* was moderately common, although it was abundant at the base of the mountain in weedy fields at the edge of the thorn forest. This particular situation is further discussed under *tectatus*, where we hypothesize that *tectatus* is better at penetrating the thorn forest, or may actually exclude *paloviridis* from that habitat.

Paloviridis has been found with *psolus, nigrofasciatus,* and each of the subspecies of *contilus,* often in the same bush, although as indicated above this may represent an overlap rather than identity of habitat preferences. These species are common in and at the edge of thorn forest and only rarely occur in the more open habitats occupied by *paloviridis*. At the southern end of the range of both species, *paloviridis* altitudinally overlaps *psolus* only slightly at the 700 foot level at 19.5 mi SW Cosalá. *Paloviridis* is common at lower elevations to the south and west, and *psolus* at higher elevations to the north in the vicinity of Cosalá.

Between Culiacán and Mazatlán, *paloviridis* is also sometimes found with *poecilus*. The narrow zone of overlap (10 miles) along the main highway and the abundance and continuous distribution of each species north and south of this zone suggest some form of interaction, possibly competitive exclusion, although the habitat of the two may differ slightly. This is more fully discussed under *poecilus*.

Paloviridis occurs with *tridens* at a number of the localities (Table 19, p. 104). The collections have all been made at the edge of the thorn forest where *paloviridis* is the more abundant, although at one locality, 51.7 mi SE Culiacán, *tridens* penetrated farther into the thorn forest than *paloviridis*.

The altitudinal range of this species has not been adequately determined. At least at the southern end of its range it was not found over 700 feet in a transect up to 1500 feet in the vicinity of Cosalá. No other mountains have been investigated in its main range (north to Los

Mochis). It has not been found in the foothills near Tezopaco nor well into the Sierra Madre near Alamos, but in this region it is rare even on the coastal plain.

SEASONAL OCCURRENCE.— Our earliest record for *paloviridis* is 3 August at 21 mi SE Guaymas. At Culiacán in the same year (1970), the species did not mature until the middle of August in fields under observation since the end of July. South of that city we have several records of teneral adults in the middle of August. In 1964 Cohn worked briefly in the Culiacán-Mazatlán region in late July without finding any *Barytettix*. The rains at least in Culiacán were late that year and the first shower had occurred only about a week before. A similar brief investigation of a few *Barytettix* localities in mid-June 1971 before the summer rains similarly yielded no *Barytettix*. It seems likely, therefore, that the eggs of this as well as other species in the Sinaloa-Nayarit region hatch with the first summer rains in late June or early July and that the animals mature a month or two later.

Our latest record for the species is 28 November at 1.1 mi SW San Ignacio Ferry and 64 mi SE Culiacán, and 1 December at 21.2 mi N Los Mochis turnoff. Although the species was not common at either locality, the abundance of other species of *Barytettix* there suggests a somewhat longer life. No collecting for *Barytettix* in the range of *paloviridis* has been done in the winter or spring.

DISTRIBUTION.— The northernmost record for *paloviridis* is 68 mi S Hermosillo, Sonora, and the southernmost, 20 mi N old Mazatlán Airport, Sinaloa. North of Los Mochis the species apparently occurs in scattered colonies and has not been found east of the main highway on two roads investigated (Alamos and Tezopaco regions). South of Guamúchil it is almost continuously distributed along the main highway to 63 mi NW old Mazatlán Airport. Along the highways south of this locality we have only two males from 30 and 20 mi N Mazatlán, although the species is fairly common farther inland on the San Ignacio road, about 49 mi N Mazatlán. Within its main range south of Guamúchil, *paloviridis* occurs as far east as we have investigated in the vicinity of Tepuche, Sanalona and San Ignacio, but all of these collections have been in the coastal plain or low foothills. It is absent from around Badiraguato. In the only area within its main range for which we have a transect

into the mountains, it was found no farther inland than 19.5 mi SW Cosalá. The limitation may have been altitudinal or from interaction with *psolus* which occurs commonly from this point inland and at higher elevations.

RECORDS.— Specimens examined: 512♂♂, 89♀♀, 2 juveniles and many more reared to maturity. A complete list of the records of this species will be found in Table 19, p.104.

THE HUMPHREYSII GROUP

The remaining *Barytettix* populations are much more diverse from one another than are the members of the Psolus or Crassus Groups. Some are the exclusive occupants of the northern end of the generic area, and the rest extend far into the middle of that range where they are sympatric with members of the Psolus Group. Although these populations do not share among themselves any single outstanding characteristic, they lack any of the more distinctive features of either the Crassus of the Psolus Groups. Nevertheless, the cercus, aedeagus, bursa, and thick tube are constructed on the same general plan which is somewhat different from that found in the other species groups. Relationship can also be demonstrated between the most highly divergent elements by hybrid or intermediate populations. We are therefore designating these taxa as members of a third species complex, the Humphreysii Group.

Two species have been previously recognized in this complex, *humphreysii* and *cochisei,* both from Arizona and now known from Sonora. We now have evidence of hybridization of the two forms from one area in Arizona and from another about two hundred miles to the south in Sonora. Therefore, *cochisei* is here reduced to subspecific status, even though critical problems remain concerning its biological status. The nominate subspecies displays an extraordinary amount of variation throughout its range in Sonora. Much of this variation is discordant, suggesting differential gene flow and selection rather than past or present restriction of gene flow between populations, and thus not worthy of subspecific recognition. In southern Sonora, however, a series of morphological and color changes takes place concordantly. Although intermediate conditions or tendencies toward southern conditions are found just north of the point of change of several of these characters, the gap between the two morphotypes has now been narrowed to 3.4 miles, and neither hybrid

populations nor evidence of introgression has been found. We are therefore recognizing the southern populations as a separate, new species, *tridens.*

The three taxa share the features listed below. These are not restricted to the Humphreysii Group, but their combination is unique.

AEDEAGUS

1. Short and broad (as in the Crassus Group, but slightly larger) (Fig. 1 E).
2. Dorsal valves deeply cleft along the midline (except in a few variant populations of *tridens,* in which excisions laterad of the aciculate median teeth are deeper than that between the teeth) (as in the Psolus Group) (Figs. 8 F, G; 10 A-T).
3. Dorsal valves more or less flat (weakly convex in northern *humphreysii*), smooth from side to side, or very weakly fluted.
4. Ventral valves considerably wider across the middle or base than near the apex (somewhat as in the Crassus Group) (Figs. 1 F, 11 A-P).
5. Ventral valves in side view straight or slightly up-turned near apex (as in the Psolus Group), never down- or out-turned (Figs. 9 A, C, E).
6. Ventral lobes of the sheath lengthily exposed beyond the ramus of the cingulum (as in the Psolus Group), never collar-like (Figs. 1 E-F); the process of the ramus of the cingulum obscured by the sheath (Fig. 1 E).

CERCUS

1. Strongly incurved and twisted, so that the distal portion lies almost flat over the supra-anal plate (less so in northern *humphreysii*) (extreme condition seen in Fig. 8 H).
2. Disto-dorsal portion strongly produced (less so in northern *humphreysii,* but always more than in *terminalis, crassus,* and *contilus*) (Figs. 6 A-P).

BURSA COPULATRIX (Figs. 16 E; 17 E, F)

Short (but not as short as in the Crassus Group).

THICK TUBE (Figs. 16 E; 17 B, C, E, F)

Arising dorsally and proceeding dorso-cephalad, thin at and beyond origin, proximal bends shorter than bursa and not dilated (all but the first as in *contilus*).

COLOR (Frontispiece)

1. Pronotum with metazona, ventral carina, and ventral third of lateral lobes of pronotum same as ground color, without black markings.
2. Abdominal mid-dorsal longitudinal stripe and

dorso-lateral yellow and black spots always distinct.

The features listed below are found only in the Humphreysii Group, but not in all populations:

1. Ventral aedeagal valves aciculate or lengthily acute (except *h. cochisei,* Tezopaco *h. humphreysii,* and some *tridens*) (Figs. 9 B, D, F; 11 E-H).
2. Ventral valves with the medial margins concave at least in the distal half, and the lateral margins usually convex, thus the valves distinctly, and often strongly, incurved (except *h. cochisei* and Tezopaco *h. humphreysii*) (Figs. 11 E-H, J-P).
3. Ventral lobes of the sheath (always lengthily exposed) in ventral view truncate or only broadly and briefly produced, never with approximate finger-like projections (except in *tridens* which possesses finger-like, but widely separated projections) (Figs. 12 A-S).
4. Apices of the ventral lobes of the sheath in distal view flattened, and more or less straight across (except in *tridens* and Tezopaco *h. humphreysii*), never oval and parallel.

Table 13 under the diagnosis of *humphreysii* will serve to differentiate the two species of this group.

Barytettix humphreysii (Thomas)

Included in this taxon as a subspecies is *cochisei* Gurney, for reasons discussed under Geographic Variation and more extensively under *cochisei.*

DIAGNOSIS.– Because of the extensive geographic variation in this species, no one character (with the possible exception of the visibility of the ventral valves), or even a combination of characters will serve to distinguish *humphreysii* from *tridens.* However, a number of characteristics are restricted to one or the other species, even though they are not found throughout the species in which they are present. On this basis, Table 13 may be used to distinguish all males, but only some females of the two species. Note particularly that the middle column has been included for completeness, but cannot be used for identification.

Color comparison of all species of the genus may be found in Table 3, p. 25 . Geographic variation in color and other characters in *h. humphreysii* may be found in Table 14, p. 68 , and in

h. cochisei in Table 15, p.79 . Brown specimens of *humphreysii* may be readily recognized from the brown species of the Psolus Group by the lack of the distinctive pronotal markings of the latter. The brown variants of *paloviridis* in the Guaymas area are indistinguishable in color from the nearby brown *humphreysii,* and the green *humphreysii* in southern Sonora are similarly indistinguishable from sympatric green *paloviridis.* In the latter region, however, in contrast to the reddish or reddish-purple unicolored tibiae of *paloviridis, humphreysii* often has some blue on the tibiae which are often distinctly bicolored. Green *humphreysii* is indistinguishable in all color characters except tibial color from *poecilus* and *crassus* which are found far to the south. In these cases where color identification fails, male *humphreysii* may be distinguished from members of other species groups by the twisted, expanded cercus, and from *paloviridis* and other members of the Psolus Group by the absence of an enlarged pallium.

SPECIES DESCRIPTION.— CERCUS (Figs. 6 A-K): incurved, twisted, dorsal margin concave, disto-dorsal portion enlarged, each character moderately so in north, strongly so in south; when strongly twisted and incurved, disto-dorsal portion lies horizontally in normal resting position (similar to Fig. 8 H); disto-ventral portion acute angulate, often moderately produced, rarely rectangulate. AEDEAGUS (Figs. 1 E-F; 9 A-D): short (length 0.05-0.12 times length of pronotum) (or moderately elongate, 0.11-0.14 times length of pronotum in *h. cochisei*), wider than long (length 0.57-0.69 times width, 0.82-0.84 only at 48 mi S Hermosillo and 74.4 mi S Navojoa; 0.74-0.87 in *h. cochisei*). DORSAL VALVES (Figs. 8 F-G, 10 A-R): moderately convex from side to side, to more or less flat and sometimes weakly fluted longitudinally; free lobes broad and divergent, or parallel, or narrow and convergent (narrow, parallel and widely separated in *h. cochisei*), medial margins smooth or with small to large obtuse teeth, or large acute teeth, margins forming a V or a narrow U between teeth and either strongly divergent or convergent distad of teeth (margins forming a broad U or V in *h. cochisei*); lateral margins weakly to strongly convex, often divergent, apices broad and blunt to narrowly acute. .VENTRAL VALVES: in cephalic view (Figs. 8 F-G), dorso-lateral portions in north more widely separated than ventral portions, thus widely exposing ventral wall of phallotreme, in south dorsal and ventral portions about equally separated; in caudal view (Figs. 9 B, D; 11 A-M), lateral margins always converging distad, convex in proximal half, convex, straight or weakly concave in distal half (margins conspicuously concave beyond base in *h. cochisei*), medial margins concave distad, and strongly (in north) or weakly (in south) convex proximad (straight and divergent in Tezopaco specimen, straight and almost parallel or slightly divergent near apex in *h. cochisei*), apices sharp acute to acuminate (usually narrowly rounded in *h. cochisei*), ventral surface longitudinally concave (Fig. 9 B) in north and south, or abruptly thickened near middle in Tezopaco-Obregón-Navojoa region, medially strongly excavate longitudinally below ventral phallotreme wall in Esperanza-Tezopaco specimens (Figs. 11 I-J); in side view, valve straight and moderately thick in north (Fig. 9 A), elsewhere variously straight or sinuate, thin or thickened at shoulder (Fig. 9 D) or near middle. RAMUS OF CINGULUM (Figs. 1 E-F): ventro-distal portion narrow, ending considerably proximad of

TABLE 13

COMPARISON OF *BARYTETTIX HUMPHREYSII* AND *BARYTETTIX TRIDENS*

Character	Conditions restricted to *humphreysii*	Conditions common to both *humphreysii* and *tridens*	Conditions restricted to *tridens*
GROUND COLOR	Green; gray; blue-green	Brown	Blue (Frontispiece)
TIBIAL COLOR	Yellow; orange; red	Purple	Blue (Frontispiece)
TIBIAL COLORATION	Bicolored	Unicolored	
DORSAL VALVES			
Attitude of free lobes	Broad and divergent or parallel (Figs. 10 A-Q)	Narrow and convergent (Figs. 10 R-T)	
Dorsal surface	Strongly and evenly convex	Flat; weakly and irregularly convex; weakly fluted; somewhat concave	
Apices	Blunt (Figs. 10 F-Q)	Acute (Figs. 10 R-T)	
Median teeth	Rounded; obtuse; absent (Figs. 10 A-L)	Acute (Figs. 10 M-O, Q-S)	Aciculate (Figs. 10 T)
Plane of apices and median teeth	Both on same plane	Apices raised, median teeth depressed	
Inner margins of latero-apical teeth	Forming a broad U (*cochisei*) or U at least distad of median teeth (Figs. 10 A-Q)	Convergent (Figs. 10 R-T)	
VENTRAL VALVES			
In dorsal view	Apices and usually lateral margins exposed by dorsal valves (Figs. 8 F, G)		Usually completely obscured by dorsal valves (Fig. 9 F, ventral view)
Apices	Lengthily aciculate (Figs. 11 E-H, K-M) or briefly rounded (*cochisei*) (Figs. 11 A-B)	Acute or briefly aciculate (Figs. 11 I, J, N-P)	
VENTRAL LOBES OF SHEATH			
Apices	Truncate or broadly rounded (Figs. 12 A-F, K, M, N)	Narrow but not elongate (Figs. 12 G-I, S)	Appearing finger-like, lateral (Figs. 12 O-R)
Median excision	Slight and shallow (Figs. 12 A-L)	Moderate (Figs. 12 M-N, Q)	Wide and deep (Figs. 12 O, P, R, S)
CERCUS			
Disto-dorsal portion	Moderately expanded (Figs. 6 A-H)	Strongly expanded (Figs. 6 I-P)	
Disto-ventral tooth	Produced (Figs. 6 A-I, K)	Rectangulate (Figs. 6 J, M)	Obtuse or rounded (Figs. 6 L, N-P)
Attitude	Weakly curved and twisted	Strongly curved and twisted (Fig. 8 H)	
BURSA COPULATRIX			
Distal end	Triangular (*cochisei*) (Fig. 17 F)	Truncate (Fig. 17 E)	

junction of dorsal valves with ventral lobes of sheath, thus exposing a lengthy portion of ventral lobes. VENTRAL LOBES OF SHEATH: lengthily developed proximad of junction with dorsal valves but without strong sclerotization there (Figs. 1 E-F, 9 A-D); flat from side to side to swollen along midline; proximal portion strongly flanged (briefly reflexed) in north and south or flat in middle part of range; distad of junction with dorsal valves (Figs. 9 A-D, 12 A-N), not at all to moderately elongated; apices truncate, or rounded, or briefly and angulately produced in middle of each apex (Obregón region, Figs. 12 H-I), or moderately produced into blunt, widely separated broad processes (in south, Fig. 12 N) which are never finger-like or appressed to each other; apical portions of lobes appressed to valves in north, or projecting like lips at variable angles from valves. BURSA COPULATRIX AND THICK TUBE (Figs. 16 E; 17 B, C, E, F): bursa wider than long (length 0.66 times width) (or about as wide as long in *h. cochisei*, length 1.1 times width), pleated; proximally with a moderately or well-developed sclerite on either side; apex truncate (triangular in *h. cochisei*); thick tube undilated, arising subdistally from dorsum of bursa (or distally in *h. cochisei*), and proceeding dorso-cephalad, length between proximal bends much shorter than bursa. COLORATION: ground color green, blue-green, gray, or brown, with varying amounts of yellow, abdomen usually more yellow. Head with yellow post-ocular stripes narrow in north, wide in south. Pronotum with dorso-lateral yellow stripe narrow in north, generally broad in south, rarely extending weakly onto metazona; black spot on lateral lobe restricted to pro- and mesozona, usually completely cut by cephalic diagonal yellow stripe, caudal horizontal stripe absent to complete, spot narrowly to broadly bordered ventrad by yellow, ventral third of lobe and ventral carina concolorous with metazona (yellowish apparently only in poorly preserved specimens when ground color is yellow brown). Abdomen with mid-dorsal yellow stripe usually sharply defined, sub-obsolete only in south; yellow and black dorso-lateral markings usually well-developed; supra-anal plate, cerci, and subgenital plate tinged or strongly colored with color of base of hind tibia. Hind femur with ventral half of pagina yellow or green, dorsal half darker green, blue-green, brown or blackish, sometimes entire pagina green; geniculae usually tinged with color of base of hind tibia, with black lunae. Hind tibia unicolored yellow, orange, light red, wine, or purple; or bicolored, bluish or purplish proximad, gradually becoming purple or reddish distad. MEASUREMENTS (in mm): those of the series studied are summarized in Figures 19 and 20.

GEOGRAPHIC VARIATION AND SUBSPECIATION.— This species displays a complex pattern of variation in which two types appear to be distinguishable. All specimens from southeasternmost Arizona and from a small area south of Hermosillo in Sonora possess a number of distinctive aedeagal and bursal features. These characteristics are concordant in marginal populations of this morphotype which are found within 10 to 20 miles of other *humphreysii* morphotypes, with the exception of two hybrid populations near Bisbee, Arizona and two south of Hermosillo, Sonora. The hybrid zone is very narrow, and individuals only two to six miles away appear to be unaffected by the hybridization. One of the hybrid populations is considerably variable. We interpret these data on concordance and hybridization as evidence for recent contact between two previously isolated

populations, thus satisfying our definition of subspecies. The southeastern Arizona form was described by Gurney (1951) as a full species, *cochisei*, which we here reduce to subspecific status and include within it the Hermosillo populations. Certain data are difficult to interpret under this concept and the possibility that *cochisei* and *humphreysii* represent stasipatric species in the sense of White et al (1967) and Key (1968) are discussed under *cochisei*, where a complete description and discussion of the hybrid populations will also be found.

The remaining geographical variants of this species do not display this degree of concordance and many show no morphologically intermediate transitions to other variants. Accordingly, these are not named, but are described and discussed under the nominate subspecies.

DISTRIBUTION.— This species occupies most of the southeastern quarter of Arizona and extends southward to northernmost Sinaloa in México. Eastward it is known from southwestern New Mexico near the Arizona border, and northwesternmost Chihuahua, but farther south in México it has not been found east of the Sierra Madre Oriental.

Barytettix humphreysii humphreysii
(Thomas)
Figs. 1 E-F; 2 A; 6 B-K; 8 G; 9 A-D; 10 F-R;
11 E-M; 12 C-N; 16 E-F; 17 B, E

Pezotettix humphreysii Thomas, 1875, Rep. Geogr. Geol. Expl. Surv. West of the 100th Meridian in charge of G. M. Wheeler, 5 (Zoology): 890-892, Pl. XLV, Figs. 1-2 [In: Rep. Geogr. Surv. West of the 100th Meridian]. [Types♂, ♀, Southern Arizona, 1874; apparently lost.]
Conalcaea neomexicana Scudder, 1897, Proc. U. S. Nat. Mus. 20:24, 26, Pl. 2, Fig. 9. [Type, ♂, New Mexico, Grant Co., Silver City; Academy of Natural Sciences of Philadelphia.] [Synonymy from Gurney, 1951.]
Barytettix borealis Caudell, 1908, Proc. Entomol. Soc. Washington 9:69-70. [Types, 2♂♂, 1 ♀, Arizona, Pima Co., base Santa Catalina Mts.; lectotype in United States National Museum.] [Synonymy from Gurney, 1951.]

The types of this subspecies probably should be in the United States National Museum where other Thomas types are now located, including that of *Pedioscirtetes nevadensis* which was described in the same paper as *B. humphreysii*. However, a search for the types was made by Ashley B. Gurney of that institution during the preparation of his revision of the *Conalcaea* complex, and he reports that the types are "apparently not in existence" (1951:299). The original

description and the figures accompanying it clearly indicate a species of *Barytettix*[16], but these are not precise enough for us to determine to which species of the genus the name applies. Thomas indicated that the specimens were collected on the 1874 expedition in "southern Arizona," a region where only *h. humphreysii* and *h. cochisei* occur. We have been unable to locate an account of the route of that expedition, and cannot determine whether it passed through the range of only one or both of the subspecies. We therefore follow Gurney's (1951) assignment of the name *humphreysii* to the more widespread of the two forms in southern Arizona.

DIAGNOSIS.— This subspecies may be distinguished from *h. cochisei* in the male by the convex outer margins of the ventral aedeagal valves, usually concave inner margins, and often aciculate apices (Figs. 11 E-M), and in the female by the truncate distal end of the bursa copulatrix, and the distinctly sub-distal origin of the thick tube (Figs. 17 B, E). South of Hermosillo, adjacent to the range of *cochisei*, the lateral margins of the ventral aedeagal valves may be slightly concave somewhat as in *cochisei* (Fig. 11 G). The dorsal aedeagal valves, although quite variable, are usually distinctively different from those found in *cochisei*. Their free lobes are usually broad and blunt (except in southern Sonora) and their medial margins are often provided with prominent teeth near the middle (Figs. 10 F-R), and distal to the teeth are never parallel, being either divergent or rarely convergent.

Body and tibial color, color pattern, and shape of cercus are identical in the two subspecies in the region of contact in the Douglas and Hermosillo areas, but elsewhere *h. humphreysii* may be distinctively different. The ground color may be bluish-green or green, the tibiae bluish-purple, the cercus may be strongly incurved and twisted, the disto-dorsal portion greatly expanded and the disto-ventral tooth rectangulate or but little produced. In addition, certain geographic variants in the ventral aedeagal valves and in the ventral lobes of the sheath differ from *cochisei*. The ventral surface of the valve may be strongly swollen in the middle, and it may be sharply excavate proximally or near the medial margin,

and the lateral margin may be uniformly thick or greatly swollen near the middle, all in contrast to the smooth but longitudinally concave ventral surface and distally thin, proximally moderately swollen lateral margin of the valve in *cochisei*. Other variants in these characters are similar to *cochisei*. In the ventral lobe, *humphreysii* has a strongly developed proximal flange in Arizona and northernmost Sonora where it is in contact with *cochisei*, which lacks the flange or has it only weakly to moderately developed. The flange is weak or absent in central Sonoran *humphreysii* (in the region where *cochisei* is also found), but it is well-developed again in southern Sonora. The distribution of the geographic variants in this subspecies is summarized in Table 14, and color comparisons with all species may be found in Table 3, p. 25 .

SUBSPECIES DESCRIPTION.— Characteristics of *h. humphreysii* are those given in the preceding species description where all characteristics found exclusively in the subspecies *h. cochisei* are enclosed within parentheses.

GEOGRAPHIC VARIATION.—This subspecies displays strong geographic variation in almost every character studied. Table 14 is an attempt to summarize these data visually in order to demonstrate the degree and location of concordance among the variants.

Most of the localities listed in that table represent a series of closely spaced collections along the main west coast highway between Nogales and Los Mochis. Between Guaymas and Los Mochis (SE Navojoa) the highway runs roughly through the middle of the coastal plain. Material from transects and localities to the east of this road is listed in indented portions at the appropriate geographical position in the list. The variation in each character is indicated by words, abbreviations in capital letters usually of the first letter of the condition, or by letters referring to figures. In the latter case, conditions which we consider to be individual variants of the same basic structural type are listed in parentheses. All such variants are listed for the first locality at which the basic type occurs, even though the variants may not occur there, and they are not repeated for subsequent localities where they do occur. This has been done to make the discontinuities clearly visible in the table. Solid horizontal lines in the character columns represent major discontinuities, dashed

---

[16]Emarginate caudal margin of pronotum; abbreviate, narrow, spatulate tegmen; falcate and distally enlarged male cercus; conical male subgenital plate; interrupted black spot on lateral lobes of pronotum; robust form.

TABLE 14

GEOGRAPHIC VARIATION IN *BARYTETTIX HUMPHREYSII HUMPHREYSII*

Locality (distances in miles)	COLOR				CERCUS	AEDEAGUS								
						Dorsal Valves		Ventral Valves			Ventral Lobes of Sheath			
	Ground Color	Pronotal Stripes	Paginal Stripe	Hind Tibiae	Shape Fig. 6	Dorsal Surface	Shape Fig. 10	Shape Fig. 11	Thickness	Apical Lipping	Shape Apices Fig. 12	Proximal Flange	Width	
Central Arizona (Prescott – Portal – Nogales)	BG	Narrow	Strong	Y (O, R rare)	B (C–F)	Convex	F (G–I)	E (F)	Thick along margin	Flat	C (D)	Strong	Long	
Southeastern Arizona (Pierce-Huachuca Mts region)				Y, O, R										
Nogales – 17.7 N Imuris				Y										
14 – 6.1 N Imuris				Y, O, R										
3.4 SW Imuris				R										
50 S Santa Ana	BG	Narrow		R										
32 N Hermosillo	O	Broad		R									Intermed	
14 N Hermosillo	O	Br., Nar.		R, W										
11 N Hermosillo	BG	Intermed.		R	B	Convex	F / J	F	Thick along margin	Flat / Intermed.	Intermed / C		Intermed.	
b. cochisei Hermosillo – 14.6 S														
39 S Hermosillo	O	Broad		P	G (H)	Flat or Fluted		G (H)	Thick at shoulder	Flat, Intermed.	F	Strong	Broad	
40 – 48 S Hermosillo				R, W, P			J		Thick at shoulder	Fl, Intermed. Lipped		Strong, Weak		
b. paloviridis 18 N Guaymas				W										
5 – 4.2 N Guaymas	O			W			K (L–M)		Thin, Intermed.	Lipped		Weak		
Saladita Bay, 4 W Guaymas	Bluish								Thin Intermed.					
b. paloviridis 8 – 21 SE Guaymas														
17 – 22 SE Guaymas	BG			W					Thin					

Locality									
33 SE Guaymas	Green	—	P–W	—	Intermed.	—	—	—	
37 – 38 SE Guaymas	—	—	W, P–W	G	Thin, Intermed.	—	—	—	
25 WNW Obregón	Green	Broad	W	I	Intermed.	G	—	F, Broad	
10 NW Obregón	Green	O	W		Mixed	Mixed	O (N, P, Q)	Mixed	Intermed.
NW Esperanza		Broad	P–W		Medially thick	J		H	Intermed.
Tezopaco	BG?	Narrow?	W?		Medially thick	I		G	
10 SE Obregón	Green	Broad	P–W	Strong?	Medially thick	K (L)	K (L)	H (I, J), Intermed.	Intermed.
21 SE Obregón	—	—	W, P–W	Strong, Weak	Med. thick, Intermed.				
22 NW Navojoa	—	—	W, P–W	Strong, Weak	Med. thick			H	Weak
6.8 NW Navojoa	Green	Broad	W	Strong	Med. thick, Intermed.	K	K	K (M), Intermed.	Strong, Weak
10 E Navojoa	BG, O	Broad	P	Intermed.	Med. thick	K		K (M)	Long
13 W Alamos	O	Broad	W, P	Strong	Intermed.	—			
1 – 2 NW, 1 S Alamos	BG	Narrow	P		Thin	K			
8 E Alamos	—	—	R, P		—	(K)			
19 – 33 E Alamos	BG	Narrow	W	Strong	Thin	(K)		K (M)	Long
10.4 SE Navojoa	Green	Broad	W, P–W	J	Med. thick, Intermed.	K (L)	K (L)	K (M)	Long
14.9 SE Navojoa	—	—	W, P–W	J, I	Med. thick, Intermed.	—			
16.4 SE Navojoa	—	—	W, P, B–P	K	Med. thick	—			
20 – 21 SE Navojoa	—	—	W, P–W, B–P		Med. thick, Intermed.	—			Strong, Weak
36 SE Navojoa	—	—	W, P–W		Thin, Intermed.	—			Strong
40 SE Navojoa (Estación Luis)	—	—	W, P–W, B–P	K	Med. thick, Intermed.	K	O	K	—
51.8 SE Navojoa (Estación Don)	—	—	W	(L)	Thin	M	R	N	
74.4 SE Navojoa (Cerro Prieto)	Green	Broad	W	(L)	Thin	M	R	N	Long

lines minor or questionable discontinuities. The variation in each character is discussed below, and this is followed by a general discussion of the significance of the concordance or discordance seen among all characters.

Ground Color. — This was the most difficult character to assess because of individual variation and differences in preservation. The few notes we have on living individuals from southeastern Arizona and northern Sonora indicate that the ground color is pearly gray rather than brown. However, most dried material is brownish and even a large series of freeze-dried specimens contains brownish individuals among the gray ones. We have designated this color type as brown-gray (BG) in the table. Specimens between 32 mi N Hermosillo and Guaymas, as well as two others near Santa Ana but not separately listed, appear to be greenish and may be transitional between the brown-gray to the north and the brighter green to the south. They have been designated as olive (O) in the table. Unfortunately, most of these specimens also show an increase in yellow, and the green sometimes appears to be a bluish pigment, making precise determination of ground color difficult. The Saladita specimens are definitely bluish (but not as bright as *tridens* found much farther south). If this color is widespread in the area (our samples here are inadequate), then specimens to the north which we have called olive may be transitional to this color type. Southeast of Guaymas a pocket of small brown specimens occurs. It is interesting to note that in this area some of the *paloviridis* are also brown and small, although elsewhere that species is almost universally green and large. Southward, the shift to green is abrupt, and all specimens from the coastal plain south of 33 mi SE Guaymas are bright green. Inland and at higher elevations, specimens become browner. However, those from 10 mi E Navojoa are clearly more brown than specimens farther inland at 13 mi W Alamos. The Navojoa sample was collected from the summit of a small mountain and very late in the season. Either factor might explain the reversal in a clear west-east trend toward brown. It is perhaps significant that individuals from the southernmost collection of *humphreysii* are just as green as those to the north, although they are only about three miles from the nearest blue *tridens*.

Pronotal Stripes. — The width of the stripes is a subjective estimate. The difference between the narrow northern and wide southern types is obvious. The sample termed intermediate at 11 mi N Hermosillo is hard to assess because the ground color is considerably lighter than the adjacent populations. As in ground color there is a trend toward the northern condition inland and at higher altitudes.

Paginal Stripe. — The estimate of the degree of intensity of color of this stripe is subject to the same problems of preservation and individual variation as that of ground color. In Arizona, northern Sonora, and around Alamos the stripe is almost always present and dark. South of Guaymas the stripe is usually lighter, and from 10.4 mi SE Navojoa to the southernmost colony the stripe is usually absent or very weak.

Tibial Color. — This character seems to be much less affected by preservation than other color characters. We suspect that all tibial color will show complete integradation, and our designations are arbitrary points on a continuum, although northern Sonoran series seem to be readily divisible into discrete red, orange, and yellow catagories as in *cochisei*. Specimens have not been compared to a color standard, but rather to adjacent populations. In Arizona, red-legged individuals occur almost exclusively in the southeastern corner adjacent to the range of the primarily red-legged *cochisei*, although a few pale red or orange-legged individuals occur west of the Pajarito Mts. Not all the southeastern specimens are red-legged, and some closest to *cochisei* (Bisbee, Portal) are yellow or pale orange. On the other hand, the hybrids between *humphreysii* and *cochisei* in this region are red. The shift to red may come at the Mexican border in the Naco region as evidenced by the all red-legged populations at that town and near Cananea. However, 130 miles south of the border in the mountains 30 mi E Carbó (not listed in Table 14), a small collection of females contains yellow, orange, and red-legged specimens. This may be an altitudinal effect, because the transition on the main highway to the west occurs only 43 miles south of the border at Imuris. South of Imuris all specimens in numerous collections possess red or darker tibiae. In the Hermosillo region, tibial color shifts to purple or wine. It is tempting to ascribe this shift in *humphreysii* to introgression from *cochisei* which is largely bicolored purple-wine in this region as are the hybrids between the two subspecies. However, purple or wine colored tibiae are found continuously from

Hermosillo to the southern end of the range of *humphreysii* which is far beyond any indication of morphological influence of *cochisei* on *humphreysii* (see discussion below under Ventral Valves). The irregular variation south of Cd. Obregón is hard to assess. The irregularity may be the result of sampling error; most of our series in this region are small and several color types are present. It is possible that there is here a trend toward the blue tibiae of *tridens* found farther south. Such a trend is clearly reversed in the southernmost *humphreysii* populations at 51.8 and 74.4 (Cerro Prieto) mi SE Navojoa, where all 23 specimens are wine-legged. Thus, the *humphreysii* colonies closest to *tridens* are more different from that species than are colonies farther north. This may be a case of character reinforcement, although the two species are not known to be sympatric at the present time (the closest known colonies are only 3.4 miles apart).

In the table, the following abbreviations for tibial color have been used: Y, yellow; O, orange; R, red; W, wine; P, purple; P-W, purple proximad, wine distad; B-P, blue proximad, purple distad.

Cercus.— Toward the south the cercus becomes more incurved, the disto-dorsal portion higher, and the disto-ventral tooth shorter and more rectangulate, as illustrated in Figures 6 B-K. South of Hermosillo there appears to be a minor change to a more expanded disto-dorsal portion and a more down-turned tooth (G) compared with those to the north (B-F). Between Obregón and Navojoa (and inland to Tezopaco) the disto-dorsal portion is distinctly higher (I), and the distal margin becomes almost vertical. South and east of Navojoa there is a more distinct break. Here, the disto-dorsal portion is greatly expanded, and the disto-ventral tooth reduced, and often rectangulate (J). Southward from Navojoa, the disto-dorsal portion is somewhat less expanded, and the tooth often slightly produced (K). At 51.8 mi SE Navojoa and at Cerro Prieto, 22 miles farther south, the disto-dorsal portion expands more gradually and thus appears broader, and the tooth is more rectangulate. This condition is very similar to that in the nearby *tridens* colonies and is indicated in the table by (L) although that figure is one of a *tridens* specimen. There is little difference between these southern *humphreysii* and *tridens*. The cerci of the latter are slightly more incurved, the distal margin often somewhat rounded, and the tooth often obtuse.

Dorsal Valves of Aedeagus: Convexity.— The valves of northern specimens are uniformly convex, even distally, and sometimes appear to be weakly inflated; these are given the designation Convex. South of Hermosillo the valves are somewhat flatter and each free lobe usually has a weak longitudinal concavity distad; the edges are therefore slightly turned up. In the Guaymas region and southward each free lobe is more or less flat or slightly fluted, and the two lobes together often form a flat surface. The Hermosillo and Guaymas types are too variable to be distinguished, and they are grouped together under the designation Flat or Fluted. The transition from the northern to the Hermosillo type is abrupt.

Dorsal Valves: Shape.— Despite considerable individual variation, five basic types may be distinguished, as illustrated in Figure 10. Type F of Table 14 (Fig. 10 F) is characterized by broad, blunt-tipped free lobes, the axes of which appear to be divergent. The median notch proximad of the teeth is almost always V- rather than U-shaped. There is much variation in the median teeth. They are usually blunt (I), sometimes acute (F), and occasionally entirely absent (G). Type J has unusually prominent median teeth, and the free lobes distal to the teeth are somewhat concave on their inner margins, and thus rather narrow; these characteristics may be the result of introgression from nearby *h. cochisei*. Type K has the free lobes still appearing divergent, but the lateral margins have a prominent bulge and the median notch proximad of the teeth is usually U- rather than V-shaped. In type O the axes of the free lobes have shifted to parallel or slightly convergent. The apices given the appearance of being smaller, probably the result of a distal displacement of the median teeth. The latter teeth are variable, but often constant within any one locality; thus the Tezopaco and Esperanza specimens are characterized by broad, prominent teeth with broad, ragged lateral margins (N and less frequently as in O), whereas the teeth in the Alamos population are almost always greatly reduced and often absent altogether (P). The final type (R) is very similar to that found in *tridens*, characterized by long, narrow, incurved lateral teeth, and acute, almost approximate median teeth.

If the series is examined for overall pattern, there appears to be a trend southward in a gradual shift of the axis of the free lobes from divergent to convergent accompanied by a narrowing of the lateral apices and median teeth. This trend continues almost without a break across the *tridens* species boundary. The only difference between the adjacent colonies of the two species is the final development of aciculate and possibly fused median teeth. Curiously, the more distant middle populations of *tridens* have acute median teeth (S) much like those of southern *humphreysii* (R), whereas the northern and southern populations of *tridens* possess the most extreme development of these teeth (Fig. 10 T).

The changes between the major types discussed above are relatively abrupt, and nowhere do we have obvious intermediates or populations polymorphic for two of the basic types. Although individual variation may cloud our identification, it seems clear that the transition zones must be quite narrow, or are of short duration before one or the other type is established in the population.

Ventral Valves: Shape. — Several distinctive variants occur in this structure, but, except in the north, the location of the boundaries, if any sharp ones exist, have not been adequately identified in this study. Between the northern type (Figs. 11 E-F, 9 B) and that found south of Hermosillo (Fig. 11 G) there is a very sharp break. The valves in colonies closest to *cochisei* south of Hermosillo appear to be precisely intermediate between the two subspecies (compare Figs. 11 B and F with G), and may well be of hybrid origin. The characteristics of these valves are uniform from 39 to 48 mi S Hermosillo, and the general type persists as far south as 10 mi N Obregón (Figs. 11 H, 9 D). Both the Hermosillo type and the type found farther south occur at that locality. In the southern type the valves appear more strongly bent inward, and the inner margins more strongly but more briefly concave (Fig. 11 K). Between Alamos and 40 mi SE Navojoa the outer margin makes an almost angulate bend. At 51.8 and 74.4 (Cerro Prieto) mi SE Navojoa, both margins are more gently curved and the valve appears longer (Fig. 11 M). In addition to these types, two others exist inland. At Tezopaco the valves are distinctive in their barely curved outer and straight inner margins (Fig. 11 I), but this may be a modification of the Hermosillo-Guaymas type. East of Alamos the

apical half of the valve is much narrower and straighter, and the proximal shoulder of the inner margin more prominent. Although this type is not illustrated, we have designated it as (K) in the table.

Ventral Valves: Thickness. — Various portions of the ventral valves are thickened in different parts of the range of *h. humphreysii,* but only near the southern end are they conspicuously and broadly thickened. In the north the entire length of the lateral margin appears somewhat thickened (Fig. 9 A), which is partly the result of a slight curling of the edge of the valve. South of Hermosillo only a small portion of the margin at the shoulder is thickened (somewhat as in Fig. 9 C). From the Guaymas region to 25 mi WNW Obregón the valves are usually thin, but several specimens show some thickening at the shoulder. From Tezopaco (NE Obregón) to the Navojoa region the valves are conspicuously thickened in much of their visible distal portions, as indicated in Figures 11 I and J, and distad of the dashed lines in Figures 11 K and L. The swollen portion extends from near the medial margin to the lateral margin, and is conspicuous in disto-lateral view. The apices in this view taper rapidly to aciculate points. The thickest valves are found at Tezopaco (Fig. 11 I) where the swelling is accompanied by a striking medial excavation. Proximally the valves become abruptly thinner, forming an almost rectangulate ridge. Farther south specimens from 27.8 mi NE Esperanza are intermediate between the Tezopaco condition and the less swollen, less excavate type found south of Obregón. A small collection from 10 mi NW Obregón contains specimens with thin, intermediate and thick valves. Eastward from Navojoa the valves become thinner, and they have more or less returned to the thin northern condition at Alamos and in the mountains to the east. Thick valves persist but with some variation to 40 mi SE Navojoa, and become thin again in the southernmost colonies at 51.8 and 74.4 (Cerro Prieto) mi SE Navojoa.

Ventral Lobes of Sheath: Apical Lipping. — The apices of the ventral lobes may be closely appressed to the ventral valves, or the distal third to eighth of the lobes may project away from the valves at an angle often as much as 90°. Although the distal portion of the lobe is somewhat membranous, and our scoring has been done entirely on dried specimens, the sharp difference between northern flat and southern

lipped types makes us believe that the differences are not artifacts of preservation. North of Hermosillo the lobes are usually appressed to the valves (designated in the table as Flat), and a small proportion of lobes is variously lipped but rarely strongly so. Between 11 mi N and 48 mi S Hermosillo, the valves are mixed and often intermediate (with a somewhat swollen rim as in Fig. 9 D), and from the Guaymas region southward the valves are strongly lipped, with rare exceptions only northwest of Obregón.

Ventral Lobes of Sheath: Shape of Apices.— Our scoring of this character may have been influenced by differential preservation, and by the visual effect of the degree of lipping. Nevertheless a north to south trend is discernible from the more or less truncate apices (forming a straight line or broad V, as in Figs. 12 C and D, rarely with margins as rounded as in E) in the north, through broadly rounded apices (Figs. 9 D and 12 F) to briefly produced angulate apices (Figs. 12 G-J) and finally to more produced but narrowly rounded apices (Figs. 12 K-M) in the south. In the two southernmost colonies the roundly produced apices are more lateral (Fig. 12 N) and approach the condition in the nearby *tridens* (Fig. 12 O). Zones of mixed or intermediate valves are found at 10 mi NW Obregón, possibly north of Hermosillo, and just north and south of Navojoa.

Ventral Lobes of Sheath: Proximal Flange.— The sclerotized proximal portions of the lobes are obviously curled or strongly curved in the northern and the southern portions of the range of the subspecies, and flat or weakly curved in the middle of the range. Zones of intermediate or mixed conditions are found south of Hermosillo where the adjacent *h. cochisei* colonies have weak or flat lobes, and in the Navojoa region. As in the other characters, conditions which might be ascribed to *cochisei* influence (flat lobes) extend far to the south of the *cochisei* colonies at Hermosillo, although we do not know the range of *cochisei* east of the main coast highway. The proximal portion of the ventral lobe is sometimes obscured by membrane. We have often softened this membrane with ammonia, and then probed with a pin to determine the degree of curvature of the sclerite.

Ventral Lobes of Sheath: Width.— This was a subjective estimate of the length to width ratio. The lobes of northern and southern specimens appear to be longer than wide (despite the

proximal flanging of the lobe), whereas those in the Hermosillo-Guaymas region appear to be quadrate or wider than long. Apparent intermediate conditions are found north of Hermosillo, and between Tezopaco and Navojoa.

The Chihuahua Colony at Casas Grandes.— Because of the isolated position of this colony far to the east of the main distribution of the subspecies, we have not included it in Table 14. It possesses a curious combination of northern and southern characteristics which are listed, and the implications of this combination discussed, under Distribution.

Biological Significance and Taxonomic Treatment.— We have long pondered and argued the usefulness of designating various segments of *h. humphreysii* as additional subspecies based on this pattern of geographic variation. However, if such designation is to have meaning beyond mere description, it must be based on the biological significance of the variants.

North of Hermosillo only tibial color shows a distinct pattern of geographic variation, red tibiae replacing yellow at Imuris in northern Sonora. Because this is not accompanied by shifts in other characteristics in this area, we do not consider the populations worthy of subspecific designation. The shift to red tibiae may occur much farther south in the mountains as indicated by the mixed population east of Carbó, although this is the only collection of *Barytettix* in the mountains north of Alamos. The red tibiae found in the southeasternmost corner of Arizona may be the result of introgression from the adjacent red-legged *h. cochisei* (see discussion of a possibly hybrid colony at Don Luis, near Bisbee, Arizona, under *h. cochisei*).

At Hermosillo there is a striking shift in many characteristics. Much of this may be the result of introgression and hybridization with *h. cochisei*, which interrupts the range of *h. humphreysii* for about 25 miles south of that city. The two subspecies are now hybridizing freely at 30 and 36.8 mi S Hermosillo where the colonies are highly variable and contain parental types and intermediates (see discussion under *h. cochisei*). For 11 miles south of these hybrid colonies, most characteristics of *h. humphreysii* are relatively uniform. Some are intermediate between the two subspecies (ventral valves, Fig. 11 G and compare with 11 B and 11 F, the parental types; possibly dorsal valves, Fig. 10 J, compare with 10 E and 10 I). Other characteristics are similar

to the conditions in Hermosillo *h. cochisei* (tibial color, ventral lobe width, proximal flange, and possibly apices). Some of the latter shift back toward normal *h. humphreysii* conditions not far to the south. Such a situation would justify subspecific treatment, except for the irregular and non-concordant distribution of these characteristics in the area. Thus, the dorsal valves change well north of Hermosillo; the proximal flange of the ventral lobes is variable in the first colonies south of Hermosillo, then becomes even more like *cochisei* south of the point where the ventral valves have changed. The general condition of the Hermosillo ventral valves persists far to the south, although a minor change occurs at Guaymas. Thus any boundaries drawn would be arbitrary, and the establishment of zones of introgression would apply to some characters and not to others. Perhaps we are now seeing the results of a long history of hybridization and introgression, with *cochisei* having been eliminated in the south but leaving evidence of its former presence there. Interaction between the two may also be taking place to the east where we have no collections. The present evidence points to relatively free gene flow between the two subspecies in the Hermosillo region, but at different rates for different characteristics. More intensive study in this area would be rewarding. Other characteristics which shift near Hermosillo cannot readily be ascribed to interaction with *h. cochisei*. In both subspecies, ground color, pronotal stripes, bicoloration of the hind tibiae, and twisting and distal expansion of the cerci shift in this region but persist to the southern end of the range of *h. humphreysii*. A similar pattern is seen in the convexity of the dorsal valves in the latter subspecies. The shifts in these characters are also non-concordant, and no boundaries can be established which apply to more than a few of them.

There is greater concordance in the shift in characteristics northwest of Obregón. Cercus and dorsal valve shape change here, and characteristics of ventral valve shape and thickness, and ventral lobe width and apical shape are either intermediate or mixed. A meaningful subspecific boundary might be established here were it not for a series of characteristics which pass across this point unchanged, and which sometimes change not far away (ground color, pronotal stripes, possibly tibial color, and flanging and lipping of ventral lobes). More adequate collec-

tions from this area might clarify the situation.

A similar area of concordant shifts occurs in the short distance between Estaciónes Luis and Don, 40 and 53.5 mi SE Navojoa respectively. Marked changes occur in tibial color, cercal shape, dorsal valve shape, ventral valve shape and thickness, and ventral lobe apical shape. The change in tibial color might be ascribed to a reinforcement phenomenon involving the nearby *tridens*, because it represents a reversal in a southward trend toward the bluish color found in that species. Most of the changes, however, are toward conditions in *tridens*, suggesting introgression. On the other hand, some characteristics of these *humphreysii* colonies which differ from *tridens* persist across the point of change of other characteristics, suggesting free gene flow to the north. We believe that designating these southern populations may further obscure an already puzzling situation, and suggest an explanation where none now seems entirely satisfactory.

At Alamos and Tezopaco, conditions of various characters are highly distinctive. At Tezopaco there is a remarkable development of the ventral valve (Fig. 11 I) involving considerable thickening, deep excavation, and almost straight margins. The valves of a sample at 24.7 mi NE Esperanza are almost exactly intermediate between the Tezopaco valves and those of the coastal plain populations. Other characteristics are either not much different from nearby populations, or are matched by variants in those populations (as in the shape of the apices of the ventral lobes, Figs. 12 G and I). Similarly the distinctive cerci of the Alamos populations extend to the coastal plain where probable intermediates exist, and the narrowed distal portions of the ventral valves most likely represent the end of a cline. Of greater interest is the apparent development of northern color characteristics in these populations, suggesting a connection between these and northern populations in the mountains. Thus designation of these populations as a separate subspecies would probably require the arbitrary division of clines, and would obscure a possible northern contact and genetic continuity in the mountains.

HABITAT AND ASSOCIATED SPECIES.— *Humphreysii* occurs through a wide altitudinal range and in a variety of habitats. Our highest altitudinal record is 6250 feet above Carr Canyon, Huachuca Mts., Arizona, and our lowest is near

sea level southeast of Guaymas, Sonora. At high altitudes, *humphreysii* has been found well into the oak zone, and at 33 mi E Alamos it occurred in the lower edge of pine-oak woodland. Although detailed descriptions of the habitat at these higher elevations are lacking, there are indications that *humphreysii* occurs in the more open woodlands, in savannah-like formations (as near Ruby, Arizona) or rocky areas where desert or chaparral bushes intrude (above Carr Canyon, Arizona). It is conspicuously absent from moist stream bottoms in the mountains where the trees form an almost complete canopy (4.5 mi SW Portal, Arizona). Below the oak zone, this species is found in a variety of desert habitats, including low bush mesquite, desert grassland, and creosote bush. We have many collections along the main highway from Nogales to Guaymas. The species is generally common in depressions with weedy growth, but we have not checked adjacent drier areas lacking weeds. It is apparently not present in patches of almost pure grass south of Hermosillo, and may also be absent from savannah-like areas north of that city. The species is also common in thorn scrub south of Guaymas and was abundant in the edge of thorn forest-tropical deciduous forest between Navojoa and Alamos, and near Estación Luis south of Navojoa.

There appears to be no difference in habitat between *humphreysii* and *cochisei* in the Hermosillo area, and little if any difference in southeastern Arizona. In the latter region, *humphreysii* appears to occupy mountain slopes and *cochisei* the valleys (Fig. 5, p. 81), but this is probably the result of inadequate data on *cochisei* and the paucity of collections of *humphreysii* in the vicinity. Not far to the east and south *humphreysii* has been found at lower elevations in desert and desert grassland habitats. Similarly, *tridens* replaces *humphreysii* in northern Sinaloa where the two occupy similar habitats, across a gap of only a few miles of desert vegetation in which either could apparently exist.

The northern portion of the range of *paloviridis* extends deep into that of *humphreysii*, yet the two are sympatric in the same habitat at only one locality, Estación Luis, 40 mi SE Navojoa. Here, along a stream, the vegetation was dense and weedy, and trees formed an almost closed canopy much like thorn forest, the typical habitat of *paloviridis*. In a similar but drier and more open habitat 18 mi N Guaymas, *paloviridis*

has been found alone in several different years, and once in considerable numbers. This is the northernmost colony of *paloviridis* in a habitat which appears to be more suitable for *humphreysii*. The nearest *humphreysii* records are 20 miles north and 13 miles south, but intervening areas have not been investigated. South of Guaymas, *paloviridis* has again been found alone at four localities between 8 and 21 miles southeast of that city, and *humphreysii* alone only 1.6 miles farther south. (A questionable record of *humphreysii* at 17 mi SE Guaymas lies within the range of this *paloviridis* colony.) In this area, near sea level, the two species were found separately in a habitat of scattered low but often dense bushes, mesquite trees, saltbush, and roadside weeds and low bushes. It is interesting to note that *humphreysii* is very small and brownish at 22.7 mi SE Guaymas just as are some *paloviridis* between 8 and 21 mi SE Guaymas, whereas both species are green or greenish and larger to the north and the south.

Barytettix humphreysii appears to be a low altitude replacement for the closely related genus *Conalcaea*, at least in Arizona. Three of the four northernmost localities for *humphreysii* (Clarkdale, Phoenix and Globe, from Gurney, 1951) lie below 4000 ft. and the species probably occurs in desert or subdesert habitats there. No *Conalcaea* have been reported from the Clarkdale locality, but to the west, *Conalcaea huachucana coyoterae* has been reported as common at Prescott at around 5400 ft. (Gurney, 1951), and to the east, *Conalcaea cantralli* has been found above Pine and north of Payson between 4600 and 7200 ft. Not far south of Globe *coyoterae* has been collected at about 5-6000 ft. in the Pinal Mts. Surprisingly, *humphreysii* has been collected twice at or near Prescott, once apparently with *coyoterae* by Poling and Kusche in 1917. These specimens are depauperate in size and should have been collected at over 5000 ft. in pine-oak woodland or grassland if they are labelled properly. However, there is a possibility that material labelled Prescott came from a wide radius of that city and was actually collected in valleys and canyons at considerably lower elevations. Another questionable record of sympatric occurrence of these two species is Bruner's (1908) record of *coyoterae* (as *neomexicana*, see Hebard, 1935) from Phoenix where *humphreysii* has also been found. This record, from 1100 ft., is far lower in elevation than any other

for the genus *Conalcaea,* and if the specimens were not mislabelled, they almost certainly came from nearby mountains. In southeastern Arizona the distributions of *B. humphreysii* and *C. h. huachucana* are coextensive. However, at all localities for which we have good data, *huachucana* occupies higher elevations and *humphreysii* lower elevations with some overlap in the middle. Thus in a transect on the road from the desert floor to 7500 ft. above Carr Canyon, Cohn found only *huachucana* at 7500 and 6700 ft., both *huachucana* and *humphreysii* at 6250 and 5800 ft., and only *humphreysii* at nearby localities on the desert grassland floor (Fry and Sonoita) at 4700 ft. In the Santa Rita Mts. we have large series of *huachucana* alone at over 6000 ft. in the upper part of Madera Canyon and large series of *humphreysii* alone below 5000 ft. in the lower part. In the Santa Catalina Mts. we have a large series of *huachucana* alone from Summerhaven at 8000 ft., a small series of *humphreysii* alone from 4-6000 ft., and a large series of *humphreysii* alone from Sabino Canyon at the base of the mountains at 3000 ft. Similarly, *huachucana* has been found at higher elevations in the Chiricahua Mts., overlaps *humphreysii* in Cave Creek Canyon at 5360 ft. (Southwestern Research Station), and is absent from the mouth of the canyon at 4900 ft. near Portal where *humphreysii* is abundant. The difference in habitat of the two species is strikingly apparent in a side canyon (South Fork of Cave Creek) at 5280 ft., 4.5 mi SW Portal. Here in the moist shady creek bottom with rich leaf litter *huachucana* was common and *humphreysii* conspicuously absent, although the latter was present only a few miles up the main canyon and abundant 3 miles down the canyon at its mouth. We have no evidence of competitive exclusion between these two species, but Madera Canyon would be an ideal locality to study such a possibility because of its width and ease of access.

Much material of *Barytettix humphreysii* and of various species of *Conalcaea* from Arizona has accumulated at the Academy of Natural Sciences of Philadelphia. We have only superficially examined these series, and they may hold the clues to some of the habitat and distributional problems in that state.

SEASONAL OCCURRENCE.— Throughout its range *humphreysii* is common in late summer and fall. We suspect that the eggs, at least in México, are stimulated to complete their devel-

opment by the first summer rains, which begin abruptly at the end of June, and that they hatch shortly thereafter. In 1970, only middle instar nymphs were present in the Imuris region, Sonora, on 22 July, and near Portal, Arizona, on 18 July. By 3 August a few adults (some teneral) were found among the nymphs at Imuris. In 1968, at 39 mi S Hermosillo, late instar nymphs were abundant and adults few and teneral as late as 21 August. Local residents informed us that the rains were late that year. The earliest summer record for adults is 17 July reported by Ball et al (1942) for Arizona. Our latest record is 2 December, 2 mi W Alamos, Sonora, when the species was common. We know of no winter collecting specifically for *Barytettix,* and thus do not know how much later into the winter the adults persist, or whether they overwinter. Ball et al (1942) state that eggs overwinter in Arizona, but there is evidence of overwintering adults or a spring generation in the Baboquivari Mts. Several males and females were collected there by O. C. Poling in April 1924. To confirm these records, we have examined the correspondence between Poling and T. H. Hubbell who bought and labelled this material. Poling reported abundant Orthoptera on 1 December 1923, and on 4 April 1924 wrote that he had been accumulating Orthoptera ever since December. This is an area of some winter rainfall (Dunbier, 1968), and Poling reported short, mild winters. It is therefore possible that the April adults were produced from fall or winter eggs, hatched by winter rains, the nymphs developing during a warm winter and early spring. Unfortunately, there is no information on the diapause requirements of the species which might limit such a probability. To the south winter rains decrease and a spring generation is increasingly improbable.

DISTRIBUTION.— This subspecies is presently known from the southeastern quarter of Arizona and adjacent portions of New Mexico and Chihuahua, through Sonora to northernmost Sinaloa. Limiting records are as follows: northern, Verde Valley, directly north of Clarkdale, Yavapai Co., Arizona (from Gurney, 1951); western, Alamo Canyon, Ajo Mts., Pima Co., Arizona (from Gurney, 1951); southern, Cerro Prieto, 23.3 mi N Los Mochis, Sinaloa; eastern, 1.8 mi W Casas Grandes, Chihuahua. It is absent from the southeastern corner of Arizona, where *h. cochisei* is found (see Fig. 5, p. 81, on which all records of both subspecies and the hybrids

between them are indicated). A questionable record from Douglas is discussed under *cochisei.* The eastern slopes of the Sierra Madre Occidental have been inadequately investigated, and the western slopes have been penetrated at only three places: east of Alamos, northeast of Cd. Obregón, and near Cananea, all in Sonora.

The range of *h. humphreysii* is interrupted by *h. cochisei* between Hermosillo and 14.6 miles south of that city. The only two males in a collection at 30 miles south of Hermosillo are hybrids, and a larger series at 36.8 mi S Hermosillo contains hybrids and specimens almost but not quite typical of the next *h. humphreysii* colony at 39 mi S Hermosillo (see Table 17, p. 82). The region east of this hybrid zone has not been investigated. The range of this subspecies is apparently also interrupted by colonies of *paloviridis* in the Guaymas region. This is more fully discussed under Habitat.

The most puzzling feature in the distribution pattern of *h. humphreysii* is the presence of a colony near Casas Grandes in northwestern Chihuahua. Not only is this the only record of a *Barytettix* east of the Sierra Madre Occidental, but its presence there suggests that *h. humphreysii* completely surrounds *h. cochisei.* A number of the characteristics of this colony more closely match those of colonies south of Hermosillo than the features of nearby Arizona *humphreysii* (dorsal and ventral aedeagal valves, ventral lobe flange and width, see Table 14 under S Hermosillo). This suggests to us that the Casas Grandes colony is a recent invader from south of the range of *cochisei.* The few Arizona characteristics of this colony (all color features, lipping and apical shape of ventral lobes, see Table 14 under Central Arizona) might be the result of even more recent contact and intergradation with the Arizona populations through New Mexico. No collecting has been done in either southwestern New Mexico, or in the Sierra Madre Occidental east of Hermosillo, where clues to this invasion might be found. The river valleys which dissect much of the northern Sierra Madre Occidental might have served as migration routes for *humphreysii.* Alternatively, *cochisei* might have originated as a northern isolate, and the characteristics of the Casas Grandes colony could represent the original combination of features in *humphreysii* south of *cochisei* in the Hermosillo-Guaymas region. However, the parallel north-south geographic variation of the two

subspecies makes it more likely that *cochisei* was a midwestern isolate and that *humphreysii* has only recently migrated around it to the east.

RECORDS.— Specimens examined: 392 ♂♂, 367 ♀♀, 12 juveniles and several reared to maturity. MEXICO: A complete list of Mexican records of this subspecies will be found in Table 19, p.104, and Table 17, p.82,; see also Fig. 5, p. 81. Hybrids between *h. humphreysii* and *h. cochisei* are listed under *h. cochisei*, p. 84, and in Table 17, p. 82. ARIZONA: The following Arizona material has been studied by us. (We have not included ANSP material cursorily studied, or records from Gurney (1951).) YAVAPAI CO., Granite Peak, Prescott (ANSP) (1), Prescott (ANSP) (1); GILA CO., Globe (1); Pima Co., 15-20 mi S Summerhaven, Sta. Catalina Mts., 4000-6000 ft. (AMNH, UMMZ) (5), 22 mi SW Redington, 3500-4000 ft., (AMNH, UMMZ) (2), Sabino Canyon, Sta. Catalina Mts., 2600-3500 ft. (AMNH, UMMZ) (29), Baboquivari Mts., 4000 ft. (10), Baboquivari Mts., 5000 ft. (17), Sycamore Canyon, Baboquivari Mts., 3700-4200 ft. (5), El Mirador Ranch, 4 mi SW Sasabe, Baboquivari Mts., 3900 ft. (AMNH, UMMZ) (8), mouth Madera Canyon, Sta. Rita Mts., 4500 ft. (AMNH, UMMZ) (5), Lower Madera Canyon, Sta. Rita Mts., 4500-5000 ft. (AMNH, UMMZ) (24), 11 mi N Sonoita, 4700 ft. (AMNH, UMMZ) (2); SANTA CRUZ CO., 4 mi E Arivaca (7), 1 mi E Ruby (1), Yanks Springs, 4 mi SE Ruby, Pajarito Mts., 4000 ft. (1), 21 mi SE Ruby (AMNH, UMMZ) (6), 61 Ranch, 15 mi SE Ruby, 4000 ft. (AMNH, UMMZ) (3), Nogales (5), Florida Canyon, 9 mi E Nogales, 3800 ft. (AMNH, UMMZ) (5); COCHISE CO., 8 mi S Fry, 4725 ft. (5), Huachuca Mts., above Carr Canyon, 4 rd mi W Fletcher's Roundup, 6250 ft. (1), 3.5 rd mi W Fletcher's Roundup, 6025 ft. (AMNH, UMMZ) (4), 3 rd mi W Fletcher's Roundup, 5800 ft. (AMNH, UMMZ) (18), Montezuma Pass, Huachuca Mts., 6500 ft. (1), 5 mi E Montezuma Pass, Huachuca Mts., 5000 ft. (AMNH, UMMZ) (3), 3 mi N Bisbee, Mule Mts., 5500 ft. (AMNH, UMMZ) (2), 7 mi N Gleeson (1), 2 mi W Chiricahua Nat. Mon. (4), 5 mi E Cochise Stronghold (5), Paradise graveyard, Silver Creek Road, 5 mi NW Portal (ANSP) (16), Southwestern Research Station, Cave Creek Canyon, Chiricahua Mts., 5400-5500 ft. (ANSP) (3), 1.3 mi SW Portal, 4900 ft. (16).

Barytettix humphreysii cochisei
Gurney n. comb.
Figs. 6 A; 8 F; 10 A-E; 11 A-B; 12 A-B; 17 C, F

Barytettix cochisei Gurney, 1951, Proc. U.S. Nat. Mus. 101:292-296; Figs. 58 b, d, f; 64 a, b, i, m; 65; Pl. 10, Fig. 2. [Holotype ♂, Arizona, Cochise County, Douglas; United States National Museum Type No. 59155.]

DIAGNOSIS.— Males of this subspecies may be distinguished from the nominate form, as well as from all other members of the genus, by the wide U-shaped excision of the dorsal aedeagal valves and the narrow, parallel free lobes thus produced (Figs. 8 F, 10 A-E), and by the straight or slightly diverging medial margins, blunt apices, strong proximal shoulders and conspicuously concave lateral margins of the ventral aedeagal valves (Figs. 8 F, 11 A-B). The receptaculum seminis of the female (Figs. 17 C, F) is also distinctive in the following characteristics: the bursa is short, weakly sclerotized, and triangular at its apex; the thick tube arises disto-dorsally and

proceeds dorso-cephalad, and is narrow along its entire length. In Arizona the dorsal aedeagal valves of *cochisei* often have a shallow U-shaped medial notch at the base of the excision, and thus may also have small teeth there. In *humphreysii* these teeth, when present, are almost always near the middle of the medial margins of the free lobes. The proximal flange on the ventral lobes of the aedeagal sheath is moderate, weak, or absent in *cochisei*, whereas the flange is very strongly developed in all Arizona and northernmost Sonoran *humphreysii*. South of Hermosillo this flange is usually weak or absent in both subspecies.

In color characteristics *cochisei* is identical to nearby *humphreysii* colonies in both the Douglas and Hermosillo regions. Elsewhere, *humphreysii* is often distinctively different in ground and tibial color (see Table 14, p. 68). The only other brown species of *Barytettix* are members of the Psolus Group in which the distinctive pronotal color characteristics (Table 6, p. 34) are quite different from *cochisei*. Brown individuals of *paloviridis* in the Guaymas area are also similar to *cochisei*, but have dull reddish tibiae, whereas the tibiae in *cochisei* in this region always have some purple. Males of *cochisei* may always be distinguished from *paloviridis* by the more expanded and twisted cerci, and the lack of an enlarged pallium in the former species (Fig. 15 H).

SUBSPECIES DESCRIPTION.— CERCUS (Fig. 6 A): moderately incurved and twisted; dorsal margin moderately concave; disto-dorsal portion moderately enlarged; disto-ventral tooth moderately to strongly produced (but less so than *crassus*), sometimes weakly so, acute angulate. AEDEAGUS (Fig. 8 F): moderately elongate (0.11-0.14 times length of pronotum), slightly wider than long (length 0.74-0.87 times width). DORSAL VALVES (Figs. 10 A-E): convex from side to side; free lobes narrow, parallel, medial margins smooth or with basal teeth, usually more or less parallel in distal two-thirds, sometimes slightly divergent, lateral margins weakly convex to almost straight, apices narrow, blunt acute. VENTRAL VALVES: in cepahalic view (Fig. 8 F), dorso-lateral portions widely separated, straight or slightly concave, exposing most of lateral and ventral wall of phallotreme; in caudal view (Figs. 11 A-B), always with a prominent shoulder proximad, lateral margins conspicously concave distad, medial margins straight and slightly divergent, in south distal eighth usually convex, apices narrowly rounded, rarely briefly sharp acute, ventral surface longitudinally concave; in side view, almost straight in north to slightly sinuate in south, thin distad, slightly thicker proximad at shoulder. VENTRAL LOBES OF SHEATH (Figs. 12 A-B): strongly swollen along midline in proximal two-thirds in north, usually more or less flat in south (but whole valve slightly convex from side to side), sometimes weakly swollen along midline; proximal portion flat or moderately flanged; distad of junction of lobes with dorsal valves not at all to slightly produced; apices broadly rounded, truncate, straight across, or forming a broad V; apical portion usually lipped or swollen, rarely flat. BURSA COPULATRIX AND THICK TUBE (Figs. 17 C, F): about as long as wide (length 1.1 times

width), apex triangular, thick tube arising disto-dorsally. COLORATION: ground color gray or gray-brown (rarely greenish) with little yellow in north (Gurney, 1951, reports "variable intensity of olivacous green") (usually fading to brown in most dried specimens), gray-green with much yellow in south. Head with yellow post-ocular stripes narrow in north, usually wide in south. Pronotum with dorso-lateral yellow stripes narrow in north, wide in south, sometimes extending caudad briefly onto metazona; pronotal color and black spot on lateral lobes as in species description. Hind femur with pagina always with a dorsal blackish, brownish or gray dorsal stripe, and a yellow ventral stripe. Hind tibia red, orange, or sometimes yellow (Rodeo), red or sometimes orange (Douglas region), or wine or purplish (Hermosillo region); rarely bicolored in north (one specimen, possibly poorly preserved), sometimes bicolored, darker proximad, in south. MEASUREMENTS (in mm): those of the series studied are summarized in Figures 19 and 20.

GEOGRAPHIC VARIATION.— The strong north-south variation displayed by this subspecies in many of its characters is summarized in Table 15. We have as yet no material between the Hermosillo region and southeastern Arizona, and thus cannot determine whether this variation is clinal, or where the breaks occur if it is not clinal. A striking aspect of this variation is the parallelism with that in the nominate subspecies (indicated in the table by asterisks), some of which may be ascribed to introgression from either subspecies (see under Geographic Variation in *h. humphreysii*).

Within the southeastern Arizona colonies (including those from nearby New Mexico and Sonora as above) additional variation is apparent but we do not as yet have large enough series from south of Rodeo to be certain of the pattern. Color variation of the hind tibia is summarized in Table 16. Moderately developed or weak proximal flanges of the ventral lobes of the aedeagal sheath are found in equal numbers in Rodeo males, whereas specimens from the Douglas area usually have weak flanges or none at all. In the dorsal aedeagal valves all Rodeo males have prominent median teeth separated by a moderately deep notch (Fig. 10 A), and the free lobes taper weakly if at all and are apically blunt. Specimens from the San Bernardino Ranch have virtually no median teeth, and the lobes are more tapering and more acute (as in Fig. 10 C). The lobes in Perilla Mts. and Agua Prieta males are similarly shaped, but are variable and have small teeth (Fig. 10 B). Paratype males from Douglas are quite variable in the shape of the free lobes and the nature of the median teeth, which more or less encompass the variation in the other colonies (Figs. 10 C, D), and have varying combinations of these characteristics.

Some of the characteristics of the Rodeo colony might be ascribed to introgression from *h. humphreysii*, the nearest known colony of which is located at Portal, only 10 miles to the west (Fig. 5). The yellow and orange tibiae of the Rodeo colony are unique in *cochisei*, but yellow tibiae are the rule in Arizona *h. humphreysii*. The blunt apices and more prominent median teeth of the dorsal valves, and the flange of the ventral lobes may also represent *h. humphreysii*

TABLE 15

GEOGRAPHIC VARIATION IN *BARYTETTIX HUMPHREYSII COCHISEI*

Character	SOUTHEASTERN ARIZONA (Agua Prieta-Rodeo Region)	WEST-CENTRAL SONORA (Hermosillo Region)
CERCUS	*Less incurved and twisted	*More incurved and twisted
AEDEAGUS		
Shape	Long and narrow	Short and broad
Dorsal valves	Free lobes usually narrow, apices usually more acute, base of median excision usually with a brief notch	Free lobes wide, apices more blunt, base of median excision usually smooth
Ventral valves	Longer and lengthily blunt acute	Shorter and less acute
	*Lateral margins less concave	*Lateral margins more concave
	Medial margins straight to apices	Medial margins convex near apices
Ventral lobe of sheath	*Long and narrow (lobes together quadrate)	*Short and broad (lobes together much broader than long)
	*Distal margins usually truncate	*Distal margins together forming an open V
	*Swollen medially	*Flat from side to side
COLOR		
Ground color	*Gray or brownish	*Gray-green or olive
Pronotal dorso-longitudinal yellow stripes	*Narrow and inconspicuous	*Wide and bright
Hind tibial color	*Red, orange, yellow	*Purplish
Hind tibial color pattern	*Unicolored (rarely bicolored)	*Usually bicolored

*Indicates parallel variation of *humphreysii humphreysii*

TABLE 16

TIBIAL COLOR VARIATION IN *BARYTETTIX HUMPHREYSII COCHISEI*

Locality	Male			Female		
	Red	Orange	Yellow	Red	Orange	Yellow
1.3 mi E Rodeo	11	11	3	14	4	1
2 mi SW Chiricahua	3	0	0	2	0	0
San Bernardino Ranch; S end Perilla Mts; 7-10 mi SE Agua Prieta	11	0	0	21	0	0
Douglas	3	1 + (1)	(1)	4	0	0

( ) Indicates an individual with each hind tibia a different color

influences as might be the rare occurrence of acute apices and only barely concave outer margins of the ventral valves. Interestingly, there is only the vaguest hint of *cochisei* influence on the Portal colony of *h. humphreysii*. One specimen of the eleven males studied from that colony possesses strong proximal shoulders of the ventral valves, but is otherwise typical of *humphreysii*. None of the Rodeo specimens is intermediate between the two subspecies, and there is little of the variation (except in tibial color) which characterizes recent hybridization. Furthermore it is possible that the yellow tibiae in the Rodeo *cochisei* represent a trend parallel to that in *h. humphreysii* which varies from yellow in the north, through red, to purple in the south. This and other parallel trends found in the two subspecies are indicated in Table 15.

HYBRID POPULATIONS.— Our decision to reduce *cochisei* to subspecific status is based exclusively on our interpretation that two widely separated groups of populations are of hybrid origin. Each group, one in Arizona and the other in west-central Sonora, lies between populations of typical *cochisei* and typical *humphreysii* (see Figure 5 and Table 17).

In a small collection from Don Luis (3 mi S Bisbee, Arizona, including one specimen from nearby Osborn or Bisbee Jct.) six of the seven males have the ventral aedeagal valves slightly incurved distally, and in all, the apices are sharp-

ly acute (Fig. 11 C). No *cochisei* from this region (Agua Prieta-Rodeo) show any tendency toward this condition, which is somewhat similar to that in nearby *humphreysii*. In addition, two of the Don Luis males show a straightening of the concavity of the lateral margin of the valves. There is more variation in this character in nearby *cochisei* populations, but no single *cochisei* exactly matches this condition, which appears to be intermediate between the typical *cochisei* and *humphreysii* conditions. In their dorsal valves, the Don Luis specimens display a certain amount of variation which is hard to assess. All have more or less prominent, but basal medial teeth, and in all, the free lobes are relatively narrow. In several specimens, however, the lobes are somewhat broader and blunter than are found in *cochisei*, and in all Don Luis specimens the medial margins are slightly divergent beyond the teeth. All are conditions somewhat similar to those in *humphreysii*. These characteristics of the dorsal and ventral valves suggest the influence of *humphreysii*, but in each character the condition is closer to *cochisei* than to *humphreysii*. Unfortunately, we have no series of *humphreysii* within about 20 miles of this locality against which we might check these characters, although a single male six miles to the northwest is typical of the *humphreysii* in the region. It should be noted that in the ventral valves of the Don Luis specimens, there is surprisingly little variation in the hybrid character-
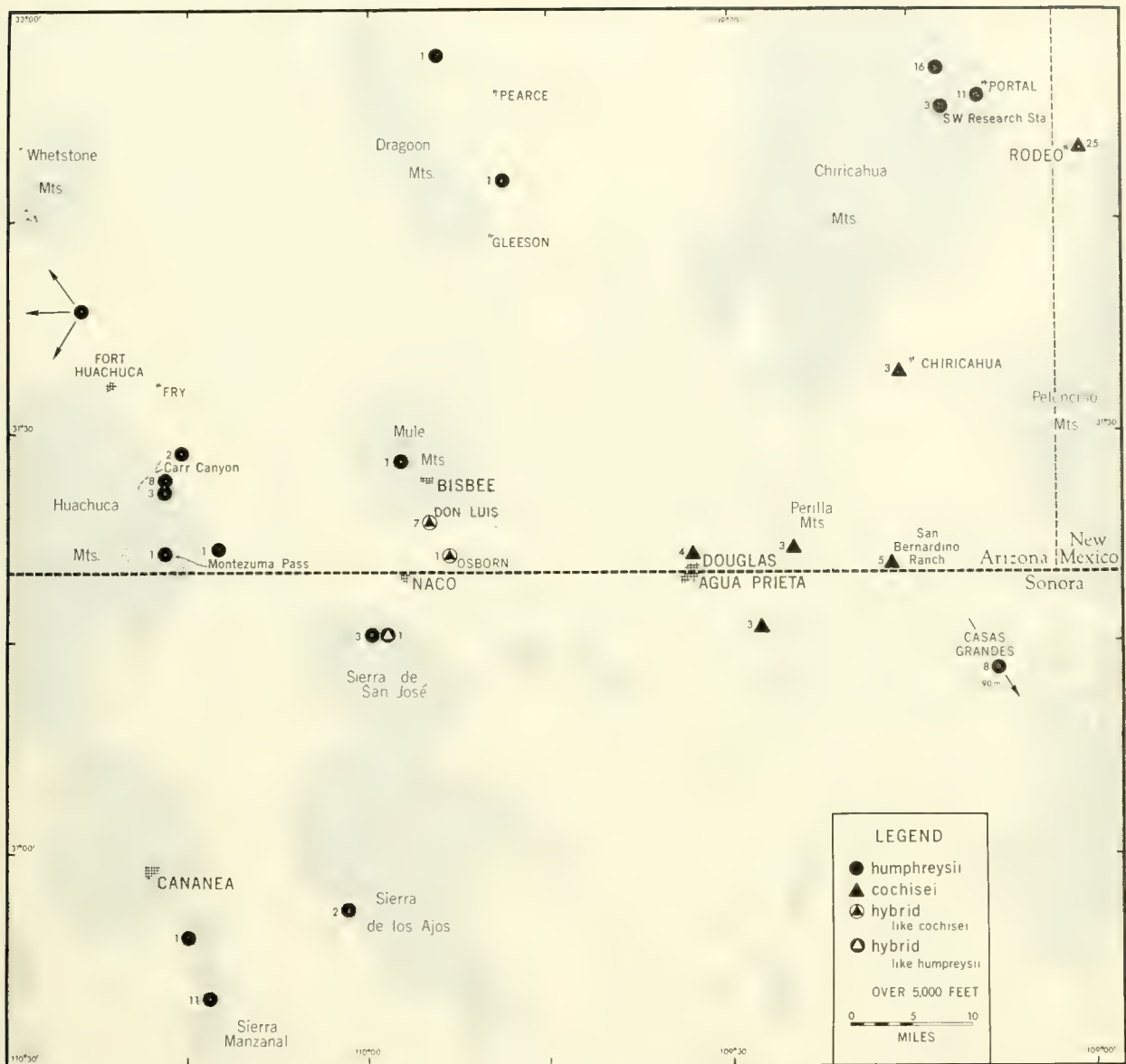
Figure 5. Distribution of *Barytettix humphreysii humphreysii* and *h. cochisei* in southeastern Arizona, adjacent New Mexico and Sonora. Large arrows indicate *h. humphreysii* collections at localities lying outside the limits of the map. Numbers accompanying symbols indicate number of male specimens from each locality.

istics. There is also some evidence of hybridity in a small collection about 10 miles south of Don Luis in the Sierra de San José near Naco. The four males from this locality are very similar to *humphreysii* from near Cananea (about 15 to 25 miles to the southwest). However, the ventral valves in one male are apically acute rather than acuminate and they lack the distinctive angulation in the medial margin (similar to Fig. 11 D) found in all the Cananea specimens. None of the Naco males have the medial teeth of the dorsal valves as prominent as those in most of the Cananea specimens, but there is considerable variation in the latter.

In the second group of presumed hybrid populations (see Table 17), that at 0.7 mi S Los Pocitos (36.8 mi S Hermosillo Cathedral) displays much more variation. The condition of both the dorsal and ventral valves in the eight males from this locality range from almost but not quite typical of the nearest *humphreysii* population, 1.9 miles to the south, to almost precisely intermediate. In two of the Los Pocitos males, the dorsal valves are almost indistin-

TABLE 17

DISTRIBUTION OF *BARYTETTIX HUMPHREYSII HUMPHREYSII*

AND *H. COCHISEI* IN THE HERMOSILLO REGION

cochisei	(2.7 mi S Hermosillo Cathedral)[1]	34.7 mi N Los Pocitos	2 ♂	6 ♀
cochisei	7.0 mi S Hermosillo Cathedral	30.4 mi N Los Pocitos	6 ♂	
cochisei	10.4 mi S Hermosillo	(26.7 mi N Los Pocitos)[1]	2 ♂	2 ♀
cochisei	14.6 mi S Hermosillo Cathedral	22.6 mi N Los Pocitos	12 ♂	17 ♀
HYBRID	30.0 mi S Hermosillo Cathedral	7.5 mi N Los Pocitos	2 ♂	2 ♀
HYBRID	(36.8 mi S Hermosillo Cathedral)[1]	0.7 mi N Los Pocitos	8 ♂	4 ♀
humphreysii	39.0 mi S Hermosillo Cathedral	1.2 mi S Los Pocitos	3 ♂	1 ♀
humphreysii	40.8 mi S Hermosillo Cathedral	3.3 mi S Los Pocitos	4 ♂	10 ♀
humphreysii	43.0 mi S Hermosillo Cathedral	5.6 mi S Los Pocitos	1 ♂	4 ♀
humphreysii	48.0 mi S Hermosillo	11.0 mi S Los Pocitos	11 ♂	3 ♀

[1]Distances in parentheses indicate calculated mileage data.

guishable from those of the nearby *humphreysii*, and the ventral valves differ from those *humphreysii* only in the shorter and less acuminate apices. In the remaining six males, the ventral valves (Fig. 11 D) are intermediate between the condition in the nearest *cochisei* population, 22 miles to the north (Fig. 11 B), and the previously mentioned *humphreysii* population (similar to Fig. 11 G). The inner margins of the ventral valves in the Pocitos males are divergent from near the base and not or barely incurved, the outer margins are convex or barely concave, the apices are lengthily blunt acute, and the shoulders in side view are slightly thickened or thin (as in *cochisei*). The dorsal valves always have the inner margins of the free lobes divergent as in *humphreysii*, but the median teeth vary from almost non-existent (almost as in *cochisei*) through prominent but short (a condition found in neither form in the area) to prominent and typical of *humphreysii*. At 7.5 mi N Los Pocitos the only two males in the collection also appear to be hybrid in having

the lateral margins of the ventral aedeagal valves almost straight or only weakly concave, the apices sharp but not acuminate, and the medial margins straight to the apices rather than convex distally or incurved. The dorsal aedeagal valves have short, inconspicuous teeth, and in one the medial margins are divergent. The two specimens are much more similar to *cochisei* than to *humphreysii* in the sum of their characteristics.

RELATIONSHIP BETWEEN *COCHISEI* AND *HUMPHREYSII*.— The data discussed above indicate that these two forms are hybridizing, that backcrossing is taking place, and that hybrids of all types are surviving in nature. The definition of subspecies is therefore satisfied, and we are treating *cochisei* and *humphreysii* as subspecies.

These same data, however, indicate that a more complicated situation may obtain. The most obvious problem in treating the two forms as simple subspecies is the interruption of the range of *humphreysii* by the pocket of *cochisei*

south of Hermosillo. It seems likely that *hum-phreysii* occupied this pocket until recently in view of its abundance to the north and south in similar habitats. If this is true, then *cochisei* must be invading the range of *humphreysii* and replacing it, indicating that while the two forms may be reproductively compatible in the short run, one or both of the parental forms may be superior to the hybrids in the long run, thus the two may be effectively isolated reproductively and represent separate species. This may also be an explanation for the narrow hybrid zones in Arizona and near Hermosillo. In both areas where hybrids are known, the distance between the two parental forms cannot be more than about 25 miles, and further collecting in the gaps will probably reduce this distance (see Fig. 5, p. 81, for Arizona, and Table 17 for Hermosillo, and note the gaps between the parental forms and the hybrids). Furthermore, in the Portal-Rodeo area the two forms are separated by only 10 miles and neither population shows much morphological influence on the other. There appear to be no major physical or vegetational barriers to the movement of these grasshoppers in these areas, and one would expect relatively free gene flow. Finally, the uniformity of the shape of the ventral aedeagal valves in the hybrid Don Luis-Oborn population suggests some sort of stabilization of hybridization, rather than the free gene flow expected if there were complete compatibility of the two forms. But under this concept, that the two represent species, one would expect parental types to outnumber hybrids wherever hybridization is occurring and one species to be replacing the other. This is not the case at two of the hybrid localities where we have the largest, though still inadequate series. At Don Luis-Osborn all eight males are hybrid, and at 30 and 36.8 mi S Hermosillo, 10 of the 12 males are hybrid, and the two of parental type are *humphreysii*, not the presumably replacing *cochisei*. At the third locality, the Sierra de San José, only one male is hybrid (although all may show some effect of hybridization) and again the parental types are *humphreysii*. Further data from south of Hermosillo indicate *cochisei* influence in *humphreysii* populations considerably south of the zone of active hybridization at least along the main highway (see Table 14 and the discussion under Geographic Variation of *h. humphreysii*). These data, and those on *humphreysii*

parental types in hybrid colonies, might be considered to indicate a long history of hybridization during which *cochisei* was slowly eliminated from all but a pocket of the region south of Hermosillo. On the other hand, some of these data might be explained on the basis of recency of contact between subspecies. But it seems inherently improbable that the two forms have come into recent contact at the same time at two points 175 miles apart and 2700 feet different in elevation. Nor does this hypothesis explain the uniformity of the Don Luis-Osborn hybrids. Recent contact between reproductively compatible subspecies would be expected to lead to highly variable characters.

Although much more distributional data are necessary, the present information suggests broad contiguity between the two forms and narrow zones of intergradation. This situation may thus be an example of stasipatric speciation, a theory offered by White, Blackith, Blackith, and Cheney (1967) and modified by Key (1968). Cytological and breeding data, and more extensive information on natural hybridization will be necessary to test this hypothesis. The 1970 laboratory work indicates these forms will cross readily and both adults and nymphs are easy to rear. The area in Arizona where the two are contiguous is easily accessible and apparently not seriously affected by man. In Sonora, the areas of contiguity near Hermosillo and possibly in the Cananea-Agua Prieta region are also easily accessible.

The recently discovered hybrids between *cochisei* and *humphreysii* bring into question the efficacy of mechanical genitalic isolation in these two forms, in spite of major differences in their aedeagi and bursae. We have too few collections as yet to determine whether the hybridization is extensive in nature, or the result of single accidents followed by extensive backcrossing. This problem is discussed further in a later section on Mechanical Isolation.

HABITAT AND SEASONAL OCCURRENCE.— All known localities for *h. cochisei* in Arizona lie in valleys or the low foothills of mountains between 3780 and 4650 feet, in areas mapped as desert or desert grassland. *Cochisei* has not been recorded as occurring in mountains, but this may be the result of a lack of collections in the area. At the Rodeo locality it was common in thin weeds in a cemetery and among low bush mesquite on the sandy outwash slopes

of the Peloncillo Mts. This habitat did not appear grossly different from that occupied by *h. humphreysii* only 10 miles across the valley at Portal (see Fig. 5), although it was drier and the vegetation sparser. Southeast of Agua Prieta *cochisei* was found in foothills covered with *Baccharis* grass and acacia (V. Roth). It is perhaps significant that the localities for the northern hybrids, Don Luis, Osborn and the Sierra de San José, at 4700 to 5150 feet, are all above the known upper altitudinal limits for the subspecies. The habitat at Don Luis included short grass, creosote bush and ocotillo (from Gurney, 1951, probably from the field notes of Rehn and Hebard, the collectors). South of Hermosillo, *cochisei* is common in roadside bushes and weeds, especially pigweed, in rich desert or thorn scrub with tall bushes or trees of mesquite, paloverde, creosote, etc. At the south edge of Hermosillo it was found in dense bushes along a small water course. The hybrid colonies near Los Pocitos were found in the same type of scrub habitat with a good growth of weeds and bushes near a water course. No obvious difference was noted between this habitat and that of the nearest *h. humphreysii* colony four miles to the south for which we have adequate field notes. In this area, only weedier habitats were investigated. Here *cochisei* was often abundant, especially in pigweed, a situation identical to collections and abundance of *humphreysii* both to the north and to the south.

Our earliest record for adult *h. cochisei* is 6 August at Rodeo, and the latest, 19 October at 36.8 mi S Hermosillo (hybrids) when they were common. Abundant late instar nymphs, but no adults were found as late as 3 August at 14.6 mi S Hermosillo.

DISTRIBUTION AND ASSOCIATED SPECIES.— *Cochisei* is known only from a small area centering on the southeastern corner of Arizona (see Fig. 5), and an even smaller area just south of Hermosillo (see Table 17). Little collecting has been done east of the limiting records in New Mexico, and probably no orthopteran collecting has been done south of the Agua Prieta record (except at Casas Grandes, Chihuahua, where *h. humphreysii* has been found) or east of Hermosillo. In Arizona the southern end of the Sulphur Springs Valley (north of Douglas), the Mule Mts. and the Chiricahua Mts. have been inadequately investigated except in the Portal area. From the

Huachuca Mts. and to the west we have reasonably adequate samples which contain only *h. humphreysii*. One specimen of *h. cochisei* from Madera Canyon, Santa Rita Mts., collected by E.R. Tinkham, we believe to be mislabelled. We have not found either *h. cochisei* or hybrids in several other collections containing *h. humphreysii* or *Conalcaea* made at various points in or near this canyon. It is suggestive, however, that this Madera Canyon *h. cochisei* shows slight hybrid characteristics in the acute apices and barely incurved medial margins of the ventral aedeagal valves.

Nowhere is *h. cochisei* sympatric with *h. humphreysii*, except for the improbable Madera Canyon record discussed above, and another at Douglas. A single male labelled as having been collected at the latter locality by W.W. Jones is typical of *h. humphreysii*, although the type series of *h. cochisei*, also collected by Jones, shows little or no influence of *h. humphreysii* characteristics. Because most of Jones' insect material is labelled Douglas, it is possible that it came from a wide area around Douglas, and that this specimen was actually collected at one of the nearby *humphreysii* localities.

All males from Don Luis and Osborn are hybrid and one of the males in an otherwise *h. humphreysii* series from Naco shows some hybrid characteristics. The series from 30 and 36.8 mi S Hermosillo are mostly hybrids with a few *h. humphreysii*.

RECORDS.—Specimens examined: 59♂♂, 61♀♀, 1 juvenile and some reared to maturity. N. MEX.: Hidalgo Co., 1.3 mi E Rodeo (29) (ANSP, UMMZ). ARIZ.: Cochise Co., 2 mi SW Chiricahua, San Bernardino Valley (25 mi NE Douglas) (3) (ANSP); San Bernardino Ranch (17 mi E Douglas) (5) (ANSP); Perilla Mts. (8 mi W Douglas) (3) (ANSP); Douglas (8) (USNM, ANSP, UMMZ). SONORA: records are listed in Table 17, p. 82.

Hybrids (females not examined; entire series listed even though some males may resemble the parental types): ARIZ.: Cochise Co., Osborn (Bisbee Jct.) (1) (ANSP); Don Luis (7), (ANSP). SONORA: Sierra de San José, near Naco (9); 30 mi S Hermosillo Cathedral, T.J. Cohn 1970 No. 32 (4); 36.8 mi S Hermosillo Cathedral, T.J. Cohn 1970 No. 68 (12).

Arizona and northeastern Sonoran records of *h. cochisei*, *h. humphreysii*, and hybrids between them are mapped in Figure 5, p. 81.

Barytettix tridens[17] n. sp.
Figs. 6 L-P; 8 H; 9 E-F; 10 S-T; 11 N-P; 12 O-S

HOLOTYPE.— ♂, México, Sinaloa, 17.1 mi N

[17]From the Latin, *tridens,* the three pronged spear of Neptune, in allusion to the very similar appearance of the dorsal valves of the male aedeagus.

Los Mochis turnoff on Highway 15 (6.2 mi S Cerro Prieto), 17 October 1970 (T. J. and J. W. Cohn No. 63); University of Michigan Museum of Zoology.

We have selected the holotype of this species from a locality only three miles south of its northernmost limit for several reasons. First, it is in the range of the most distinctive geographic variant of the species. Second, the species is relatively common there. Third, the locality lies in a hill mass not likely to be seriously disturbed by agriculture or housing.

DIAGNOSIS.— Males of *tridens* may be distinguished from all other species of the genus, except the southern Sonoran populations of *humphreysii,* by the strongly twisted and incurved cercus with an expanded disto-dorsal portion (Figs. 8 H, 6 L-P), by the narrow, incurved apices of the dorsal aedeagal valves which are always provided with acute or aciculate median teeth (Figs. 10 S-T), and by the widely separated finger-like structures forming the distal half of the ventral lobes of the sheath (Figs. 12 O-S). The brown or blue ground color of *tridens* will distinguish the species from southern Sonoran colonies of *humphreysii* with similar genitalic structures but which are always green with reddish tibiae. Female *tridens* may be differentiated from all *Barytettix* species except *humphreysii* by the blue or brown ground color, blue or brown ventral third and ventral carina of the lateral lobes of the pronotum, the metazona without dark stripes, and the very short bursa copulatrix and undilated thick tube. From brown *humphreysii* females, which have a similar bursa and thick tube, females of *tridens* may be recognized by their uniformly blue or deep purplish-blue tibiae. For identification by color alone, see Table 3, p. 25 , comparing all *Barytettix* species and Table 11, p. 49 (under Geographic Variation in *psolus*), dealing with the geography of tibial color of all *Barytettix* species in the Guamúchil-Mazatlán region. The combination of blue tibiae and pronotal markings described above is unique in the genus.

Tridens may also be distinguished from *humphreysii* on the basis of a number of characteristics restricted to one or the other species, but not found throughout that species. These are set forth in Table 13, p. 65 , under the *humphreysii* diagnosis.

As indicated in the group analysis, p. 63 , and further discussed under relationships below,

p. 86 , *tridens* appears to be a southern derivative of *humphreysii,* with most of its characteristics representing relatively small modifications of those found in *humphreysii.*

SPECIES DESCRIPTION (in variable characters, condition in holotype indicated by asterisk preceding that condition).— CERCUS (Figs. 6 L-P, 8 H): strongly incurved and twisted so that disto-dorsal portion lies horizontally when in normal resting position (Fig. 8 H); dorsal margin deeply concave; disto-dorsal portion usually strongly enlarged, sometimes *forming a rounded flap, rarely only moderately enlarged; disto-ventral portion *rectangulate and *sharp, to obtuse and rounded, rarely barely produced. AEDEAGUS (Figs. 9 E-F): short (length 0.04-0.06 times length of pronotum), wider than long (length 0.48-0.63 times width). DORSAL VALVES (Figs. 10 S-T): weakly convex proximad, lateral teeth slightly turned up distad, median teeth flat or *depressed; free lobes narrow, convergent, apices narrow, *blunt or acute angulate, lateral margins *strongly and smoothly convex to apices, or strongly convex in proximal two-thirds thence weakly concave or straight (but converging) to apices, each medial margin provided at base with either a flat acute tooth much shorter than lateral tooth, or a *depressed, strongly compressed and therefore acuminate tooth almost as long as lateral tooth, the two median teeth briefly separated but parallel, or *appearing partly fused, medial margins of lateral teeth smoothly concave to apices, rarely apices slightly curved laterad. VENTRAL VALVES: usually invisible in cephalic view; in caudal view (Figs. 11 N-P), medial margins usually *evenly sinuate, concave distad, weakly convex proximad, sometimes concave from base, lateral margins always convex, apices acute or *acuminate; distal quarter twisted; ventral surface sometimes *more or less flat, but usually with either a broad longitudinal concavity appearing to result from warping of valve, or a longitudinal excavation on medial margin and valve convex laterad; valve *thin in north, thick in lateral half in south. RAMUS OF CINGULUM (similar to Fig. 1 E-F): ventro-distal portion narrow, ending considerably proximad of junction of dorsal valves with ventral lobes of sheath, thus exposing a lengthy portion of ventral lobes. VENTRAL LOBES OF SHEATH (Figs. 12 O-S): lengthily developed proximad of junction with dorsal valves but without strong sclerotization there, proximal portion strongly flanged (briefly reflexed); proximal third beyond flange flat from side to side to strongly swollen along midline; medial margins divergent from near base or *in distal half, the lobes thus appearing finger-like, widely separated, and slightly to *lengthily produced distad of junction with dorsal valves; lobes usually appressed to ventral valves, sometimes *projecting from them at an angle. BURSA COPULATRIX AND THICK TUBE (similar to Figs. 16 E, 17 B-F): bursa slightly wider than long (length 0.77 times width), weakly sclerotized and pleated, apex truncate; thick tube undilated, arising subdistally from dorsum of bursa and proceeding dorso-cephalad, length between proximal bends much shorter than bursa. COLORATION (Frontispiece): ground color *blue or brown, with varying amounts of yellow. Head with yellow post-ocular stripes always present, usually *wide. Pronotum with dorso-lateral yellow stripes broad and extending briefly onto metazona, sometimes extending as a weak yellow wash to dorso-caudal margin of lateral lobes; black spot on lateral lobes restricted to pro- and mesozona, usually completely cut by cephalic yellow stripe which is always well-developed, caudal horizontal yellow stripe in spot usually incomplete or absent, sometimes *broad and complete, spot narrowly to *broadly bordered ventrad by yellow, ventral quarter of lobe and ventral carina usually concolorous with metazona (brown or *blue), yellow only in a few southern specimens which appear to have faded generally to yellowish, never bright yellow. Abdomen with mid-dorsal stripe usually *sharply defined but sub-obsolete in apparently poorly preserved specimens; lateral yellow and black spots usually *well-developed, weak in apparently poorly preserved specimens, supra-

anal plate, cerci. subgenital plate, and often subterminal segments tinged with blue. Hind femur with pagina bright yellow in ventral half, and usually with a *blue or jet-black, sharply defined stripe in dorsal half, often weak, narrow, incomplete or absent; carinae blue or black (both in holotype); geniculae blue with black lunae. Hind tibia unicolored blue or *deep blue-purple (often deep purple, or *purplish distad when seen under strong light). MEASUREMENTS (in mm): holotype male: length of body, 36.7; length of pronotum, 8.1; length of tegmen, 5.3; length of fore femur, 6.9; length of hind femur, 19.0; maximum width of hind femur, 5.7. Measurements of the series studied are summarized in Figures 19 and 20.

PARATYPES.— Other than the holotype and juveniles, all specimens examined in this study are designated as paratypes. Male and female paratypes are deposited in the University of Michigan Museum of Zoology, the Academy of Natural Sciences of Philadelphia, the United States National Museum, the British Museum (Natural History), and the Instituto de Biología of the Universidad Nacional de México.

RELATIONSHIPS.— *Tridens* appears to be a southern isolate of *h. humphreysii*. The two forms are identical or very similar in five characteristics found nowhere else in the genus: short, truncate female bursa; sub-disto-dorsal thick tube; incurved, aciculate ventral aedeagal valves; dorsal valves with incurved and upturned lateral teeth; and greatly expanded disto-dorsal portion of the cercus. In five characters the condition in *tridens* represents an extreme development of a north-south trend in *humphreysii* (see discussion under Geographic Variation in that species) and each is unique in the genus: strongly incurved cercus; obtuse or rounded disto-ventral portion of the cercus; aciculate median teeth of the dorsal valves (northern and southernmost *tridens*); narrow ventral valves obscured by dorsal valves in dorsal view; and narrow, lateral and elongate ventral lobes of the sheath and their wide distal separation. The two also share a strongly developed proximal flange on the ventral lobes, a characteristic found in southern and northern *humphreysii* but lacking in the middle Sonoran colonies of that species. Finally, the two are identical in two characteristics more widespread in the genus, the color pattern and the narrow thick tube. Only one characteristic found throughout the range of *tridens*, the shorter ventral valves, is not foreshadowed in the nearest *humphreysii* colony. All other differences between them are found only as distinctive geographic variants; the alternative conditions in one species are identical to those in the other species (Table 13, p. 65).

That *humphreysii* and *tridens* represent different species is suggested by the concordant change in a series of characters across the 3.6 mile gap now separating the two forms. The two closest colonies differ in the following eight characters: red tibiae versus blue; uniformly green paginae versus blue and yellow striped; green ground color versus blue; longer, less incurved cerci versus shorter and more incurved; acute angulate disto-ventral cercal tooth versus obtuse- or rectangulate; acute median and lateral teeth of the dorsal aedeagal valves versus aciculate median and blunt lateral teeth; ventral valves longer than dorsal valves versus ventral valves shorter and completely covered by dorsal valves. None of our material shows evidence of intergradation in any of these characters with the possible exception of the first two. The northernmost *tridens* colonies possess deep purple-blue tibiae, which might represent a combination of the blue of more southern *tridens* and the red of southern *humphreysii*. The purple-blue seems to be much too dark for this, and the purple-blue colonies extend far beyond the possible influence of *humphreysii* to Guamúchil. Perhaps more significant is the lack or lightness of the blue stripe in some individuals from north of Los Mochis, in colonies closest to the unstriped *humphreysii*. Nearby *tridens* from the El Fuerte region and from the next southern collections at Guamúchil uniformly possess well-marked dark stripes. On the other hand, many specimens from south of Guamúchil possess a weak stripe or lack it altogether. In the absence of other evidence of hybridization in the northern colonies, it seems improbable that reduction or loss of stripes is the result of introgression from *humphreysii*.

The distance between the northernmost *tridens* and the southernmost *humphreysii* colonies was reduced to 3.6 miles in 1970. Unfortunately, our collections in the area were not large enough for us to be certain that the forms do not actually overlap there, and we have done no collecting in the gap. The habitats of the two closest colonies are different, but there is no obvious barrier between them. Thus the two forms could at least be in contact in the gap. The evidence points either to reproductive isolation or to the forms having arrived only recently in the area and not yet having made contact. The former seems more reasonable and we are there-

fore considering *tridens* and *humphreysii* as distinct species.

GEOGRAPHIC VARIATION.— As might be expected of a relative of the highly variable *humphreysii,* this species displays marked north-south geographic variation, summarized in Table 18. South of Jesús María we have no more than three males from any one locality so that some of the differences between samples there may be the result of individual variation. Although there seems to be considerable discordance and reversals, especially in the south, a shift in most characters takes place between Guamúchil and Jesús María across a gap of about 40 miles. A single brown female from 5 mi SE Guamúchil (60 mi NW Culiacán) may indicate a much more abrupt change. A similar change south of Guamúchil occurs in *paloviridis,* corresponding to the northern limit of the range of *psolus.*

The most interesting aspect of the variation of this species is the greater difference between *tridens* and *humphreysii* where they are in probable contact north of Los Mochis, than where they are far separated. Thus the striking similarity of the dorsal valves of southernmost *humphreysii* (Fig. 10 R) and *tridens* in the Culiacán region (Fig. 10 S, others are even more similar) contrasts with the marked difference in *tridens* north of Los Mochis. Similarly middle and northern *humphreysii* and southern *tridens* are brown, whereas adjacent *humphreysii* and *tridens* are green and blue respectively. It is tempting to ascribe these differences to character reinforcement in the area where the two species are in contact. However, it is not certain that the species are sympatric at the present time or that they were sympatric in the past. They are found close together in a flat area (now being extensively prepared for irrigation) close to sea level in northern Sinaloa. There are extensive lagoons ("esteros") nearby along the coast, and a very slight flooding of these might easily have isolated the ancestral species. Or the two may have been isolated by the Río Fuerte, although *tridens* now occurs north of the river. Not far inland of the area of contact the river runs almost north and south, separated from the coast by a low range of hills. In the recent past the Fuerte may well have drained eastward into the lagoons south of El Carrizo, thus separating the two species.

The ventral valves are deeply excavate in the Culiacán region in a manner closely similar to that in Tezopaco *humphreysii* (Fig. 11 I). In both cases the excavation is beneath and separated from the ventral walls of the phallotreme, and its function is obscure.

Tibial color has not been tabulated because of difficulty of analysis and the possibility that some of the differences are the result of variation in preservation. Nevertheless, there seems to be a tendency for the tibiae to be deep purplish blue in the north and lighter blue in the south. All the material from north of Los Mochis is purplish blue, but that from 6 mi NE El Fuerte (actually farther north than the Los Mochis collections but also farther inland) are dark blue with a few slightly purplish. From 14 mi S El Fuerte to 1.4 mi SE Los Mochis, the series are mixed purplish blue and dark blue. At 10.9 mi W Guamúchil the entire series is a darker purplish blue than those to the north. From that point south the tibiae are more bluish and usually lighter. The very small samples from 15.2 mi NW Culiacán are slightly darker, and those from 7.2 mi SE Culiacán and from east of Sanalona (east of Culiacán) are darker yet. Under the microscope most specimens have a slight purplish cast at least distally.

The variation in paginal striping is harder to assess because of the probably greater effect of different means of preservation, and possibly because of a more complex pattern of geographic and individual variation. As indicated above, specimens from north of Los Mochis are variable and range from having almost no dark stripes to well-marked ones. All other material from Guamúchil to northeast of El Fuerte is uniformly dark striped. The single female from 60 mi NW Culiacán and all the males from Jesús María (19 mi N Culiacán) lack stripes, but three females from the latter locality and those from San Rafael (13 mi N Culiacán) are variable but relatively lightly striped. Specimens from 15 mi NW and 7.2 mi SE Culiacán, and from east of Sanalona (east of Culiacán) have dark or jet black stripes. All specimens south of that point are light or only partly striped, with the exception of the two specimens from 6.6 mi NE Cosalá. Many of the stripeless individuals come from poorly preserved earlier collections and may have lost the stripes, but those from north of Los Mochis and two weakly striped ones from

TABLE 18

GEOGRAPHIC VARIATION IN *BARYTETTIX TRIDENS*

Localities (distances in miles)	Ground Color	Dorsal Valves			Ventral Valves		Ventral Lobes beyond junction with dorsal valves
		Median teeth	Lateral teeth	Lateral bulge	Apices	Surface	
19.9-17.1 N Los Mochis turnoff	Blue	Aciculate	Short, blunt	Present	Aciculate to narrowly acute	Smooth	Greatly extended
6 NE - 14 S El Fuerte, 1.4 SE Los Mochis	Blue	Aciculate	Short, blunt	Present	Long to short acute, rarely aciculate	Smooth	Greatly extended
10.9 W Guamúchil	Blue	Aciculate	Short, blunt	Usually absent	Short acute to aciculate	Smooth, one intermediate	Greatly extended
6 W Jesús María 1 W Tecorito (19-13 N Culiacán)	Brown	Acute	Long, acute	Present	Short acute, sometimes long acute	Deeply excavate	Moderately extended (Tecorito-greatly extended)
15.2 N Culiacán	Brown	Acute	Short, acute	Absent	Short acute	Deeply excavate	Briefly extended
7.2 SE Culiacán	Brown	Long acute or wide aciculate	Very short, acute	Present	Short, sharp acute	Deeply excavate	Greatly extended
11-18 rd. mi E Sanalona	Brown	Wide aciculate	Very short, acute	Present	Aciculate	Deeply excavate	Greatly extended
33 SE Culiacán	Brown	Aciculate	Short, acute	Present	Aciculate	Smooth	Moderately extended
6.6 NE - 19.5 SW Cosalá	Brown	Wide aciculate	Short, acute	Present	Aciculate	Deeply (6.6)* or broadly (19.5)* excavate	Briefly extended
73 SE Culiacán	Brown	Long acute	Very short, acute	Present	Aciculate	Broadly excavate	Not extended

*Numbers refer to localities at left.

the south were freeze-dried and have excellently preserved color patterns.

HABITAT, ASSOCIATED SPECIES, AND SEASONAL OCCURRENCE.— This species occupies the usual broad range of habitats as do most other species, but it seems to be absent from weedy fields and from wide weedy areas along the roadside. It was not very common at any locality south of Culiacán, where it has always been found with other species. It was common at 10.9 mi W Guamúchil in the edge of thorn forest with *paloviridis*, at 6 mi NE and 14 mi S El Fuerte in the edge of thorn forest, and was common in thorn scrub in the hills 17 mi N Los Mochis. It has been found in desert-like thorn scrub north of Los Mochis through heavier thorn forest where it seems to occur sparingly. All thorn forest investigated has been thinned or disturbed. It has been found with *paloviridis, psolus, contilus tectatus, contilus dicranatus,* and *poecilus.*

Our earliest record for *tridens* is 22 August (10.9 mi W Guamúchil) and our latest 28 November (64 mi S Culiacán) and 1 December (18 mi N Los Mochis). At the latter locality the species was common. No special collecting for *Barytettix* has been done between December and July.

DISTRIBUTION AND RECORDS.— The northwesternmost record for *tridens* is 19.9 mi N Los Mochis, the southeasternmost, 63 mi NW [old]Mazatlán Airport, both in Sinaloa. Specimens examined: 72 ♂♂, 51 ♀♀, 2 juveniles and several reared to maturity. Localities are listed in Table 19, p.104.

SPECULATIONS ON THE PHYLOGENY OF THE SPECIES OF *BARYTETTIX*

A phylogeny of modern species can only be based on the determination of primitive and derivative conditions. This has proven difficult in the genus *Barytettix* for three reasons. First, we have been unable to identify with assurance genera clearly related to the Conalcaeini. Second, many of the usable characters in the genus are relatively simple structures, making convergence difficult to determine. Finally, in the case of the elongate aedeagus in the Psolus Group, we are not sure how many of the distinctive conditions in other aedeagal and associated bursal structures are the direct results of elongation and not independent of it.

Despite these problems a reasonable case can be made for the determination of primitive and derivative conditions for three characters. The aedeagus and bursa of all members of the Psolus Group are much longer than almost any other melanopline known to us (an exception is the unrelated *Proctolabus*), and thus must be the derivative condition relative to the shorter aedeagus and bursa in the Crassus and Humphreysii Groups. Similarly, and probably associated with this character, are the elongated, approximate ventral lobes of the sheath in the Psolus Group. In this structure, the opposite condition found in the Crassus Group (lobes reduced to a narrow collar beneath the ventral valves) is very similar to that in *Conalcaea,* two

undescribed genera in the Conalcaeini, and several other west coast Mexican melanoplines as well. The ventral lobes, as well as the structure of the ventral portion of the ramus of the cingulum, are almost identical to that in *Conalcaea miguelitana,* which is widespread on the Central Plateau of México and is also the southernmost species of its genus. On this basis it is reasonable to conclude that the condition of the lobes in the Crassus Group is most primitive, that in the Psolus Group the most derivative, and that in the Humphreysii Group intermediate. In the third character the situation is not as clear. The cercus is almost straight and weakly to moderately expanded in all species but *humphreysii* and *tridens,* in which it is greatly expanded distally and strongly incurved. These latter conditions are not often found in the melanoplines and are probably derivative. However, the cerci are just as expanded (but not incurved) in two northern species of *Conalcaea.* The southern Arizonan and Mexican members of the genus (several of which are undescribed), and the two undescribed genera of Conalcaeini, have the more common unexpanded straight cerci. We therefore conclude that the *tridens-humphreysii* type is derivative.

If these inferences are correct, then the Crassus Group has retained the greatest number of primitive features. It, however, has a green color, a condition rare among melanoplines and

thus possibly derivative. It would be interesting if the color of *crassus* is brown, making that geographically isolated species the most primitive of the group. We are not certain of the color in that species because of the poor state of preservation of the available specimens. Otherwise it is impossible to determine which of the three species comes closest to resembling the common ancestor. The curvature of the aedeagus (either down- or out-curved) is unique and other differences are slight.

The isolation of *crassus* in the southern tip of Baja California raises a number of intriguing problems. It may be a relict of a much wider distribution extending into Arizona and around the head of the Gulf of California, and was forced to retreat southward with increasing aridity in the north during the middle and later Cenozoic. If so, then this goes far to explain how *cochisei*, the most primitive member of the group presumably derived from the Crassus Group (discussed below), has become so widely separated from its ancestral group. However, *crassus* must have become isolated, under this hypothesis, in the middle Cenozoic. If so, then it has differentiated remarkably little from its mainland relatives, *poecilus* and *terminalis*, while its derivative groups have differentiated enormously in the same amount of time. Alternatively, *crassus* may have been isolated by the geological events which separated at least the southern end of Baja California from the mainland and created the southern Gulf of California. Larson, Menard and Smith (1968) suggest that this may have occurred only within the last 4 million years, which again seems too long for the relatively minor differentiation seen today in the grasshoppers. More recent studies by Gastil, Phillips, Rodrigues-Torres and Bonneau (1972), seem to indicate an earlier geological separation; the problem is apparently under intensive study by geologists. This hypothesis does not help to explain the geographic origin of the Humphreysii Group, but it does offer hope for dating rates of morphological change in the Crassus Group. In this regard, it is interesting to note that *terminalis* is more different from either *poecilus* or *crassus* than *poecilus* is from *crassus*. We do not yet have adequate collections from southern Jalisco to determine the probable geographical factors isolating *terminalis* from *poecilus*. If such can be determined and their origin dated, then a comparison of rates of morphological differ-

entiation in *terminalis* and *crassus* can be made. *Crassus* could have gotten to Baja California by long-distance passive dispersal over water, an event which cannot be dated.

Despite its far northern position, the Humphreysii Group was probably derived from a *crassus-poecilus*-like ancestor. It is clearly intermediate between the Crassus and Psolus Groups in the length of its aedeagus and the development of the ventral lobes of the sheath, and it is difficult to envision its derivation from a Psolus Group ancestor. The evolution of the ancestor of the Humphreysii Group would have involved the greater development of the ventral lobes of the sheath (by elongation of the sheath or retreat of the ramus of the cingulum or both) and the greater development of the free lobes of the dorsal valves (by elongation of the lobes or the deepening of the excision between them or both), and the straightening of the ventral valves. The most primitive member of the Humphreysii Group appears to be *cochisei*. Unlike its relatives, *humphreysii* and *tridens*, it shares with the Crassus and Psolus Groups parallel, blunt ventral valves, and relatively simple cerci. In addition, the disto-dorsal orifice of the thick tube of the receptaculum seminis is more similar in position to that of the Crassus Group than is the sub-distal position in *humphreysii* and *tridens*. The brown color may also be primitive. Only in its broadly excised dorsal valves does *cochisei* differ markedly from what might be considered an ancestral aedeagal condition. In this character it shows no similarity to other species, and is probably best regarded as a more recent development. The cercus in *cochisei* is also expanded moderately, a condition foreshadowing the development of a greatly enlarged disto-dorsal lobe in *humphreysii* and *tridens*. *Humphreysii* may have developed as a western or lowland isolate from ancestral *cochisei*, and there developed its distinctive incurved, aciculate ventral valves, and sub-distal orifice of the thick tube. As it moved south, it developed a green color, and more expanded and incurved cerci (derivative conditions), and prominent median teeth on the dorsal valves. *Tridens* appears to represent the southern extension of these characteristics, often in more extreme form. The situation is not that simple, however, because the northern colonies of *tridens* possess a more extreme (derivative) condition in at least color and dorsal valves than do the southern

populations. A few possible explanations of this situation come to mind. In regard to the color, the ancestral, widely distributed *humphreysii* may have been brown, as are northern *humphreysii* and southern *tridens*. The middle populations subsequently developed a green color, and after separation, northern *tridens* further developed this into blue. We know nothing of the relationships of these pigments and it would be interesting to see if one were derivable from the other. As for the dorsal valves, the unusual aciculate median processes in northern *tridens* could represent a reinforcement phenomenon. Unfortunately, this condition extends far south of any *humphreysii* influence and we are not sure if the ranges of the two species actually overlap at the present time. It is possible that they have done so in the past, but this seems to us to be less likely. This condition of the dorsal valves may have no more special significance than any other population variant.

It is interesting to note that the proximal portion of the thick tube is dilated in the Crassus Group and thin in the Humphreysii Group. We suspect that the former condition is a derivative one because the thick tube is thin in most other melanoplines and that it represents an intragroup development after the origin of the ancestor of *cochisei*. This in turn suggests that the differentiation of the members of the Crassus Group is relatively recent, as is suggested by the small differences among them. It is also interesting to speculate on the origin of the sub-distal aperture of the thick tube in *humphreysii*. This combined with the distinctive aedeagal shape appears to form a good means of mechanical isolation from *cochisei*. However, there is no evidence that these two species overlap broadly now, and further, the mechanism seems to break down where the two are presently in contact. This is discussed further in the section on Mechanical Isolation, and in the Promising Problems section.

We have argued above that certain features of the Crassus Group are primitive because they are shared with other related genera. It is always possible that those genera are derivative from the Crassus Group, and that all may be derived from another *Barytettix* stock. Thus, the massive ramus of the cingulum of the Crassus Group and the other genera of the Conalcaeini may represent a derivative condition. A narrow ramus which does not extend to the ventral midline is the commonest type in other melanoplines and in the few genera which might be related to the Conalcaeini. This type of ramus is seen in the Humphreysii Group, the most primitive member of which, *cochisei*, might thus be the least changed descendant of the ancestor of the entire genus. This hypothesis better fits the apparently small differences among the species of the Crassus Group, suggesting recent divergence, and the probably derivative condition of the dilated thick tube of the female. It also accords better with the probability that brown ground color, as in *cochisei*, is more primitive than green, as in the Crassus Group. However, it offers no help in the problem of the very wide separation of the Crassus Group from *cochisei* whose ancestor gave rise to it, *ex hypothesi*, and does not accord well with the probability that the sheath in the Humphreysii Group is derivative and that in the Crassus Group primitive.

The Psolus Group is probably derived from the Humphreysii Group. The two groups share the derivative condition of well-developed ventral lobes of the sheath, and the greatly elongated lobes of the Psolus Group are clearly the most extreme derivative condition. No member of the Psolus Group shares any derivative character of *humphreysii* or *tridens*, with the possible exception of *paloviridis* which has a green ground color as do some of the populations of *humphreysii*. In some *humphreysii* the ventral lobes of the sheath are slightly produced in the middle or more produced laterally and thus might be considered to be a tendency toward the greatly elongated lobes in all members of the Psolus Group. The similarity seems to be small, and we do not consider it significant. On the other hand, the ventral valves in *cochisei* average longer than in *humphreysii*, they are straight and blunt acute as in the members of the Psolus Group, and the phallotreme is broadly open dorsally, much as it is in *contilus*. That species also has a shorter aedeagus than any member of the Psolus Group, a primitive condition. We therefore consider *cochisei* and *contilus* to be the links between the two groups. Another possible derivation may again be through *paloviridis* if bursal characteristics are considered. The distodorsal aperture of the thick tube of that species occupies the same position as it does in *cochisei*. It is easy to envision the development of the bursa in the ancestor of the Psolus Group starting in a *cochisei*-like form with the elongation of

the bursa and aedeagus followed by a ventral-caudal bending of the thick tube, and being completed with the ventral and caudal displacement of the orifice of the thick tube. In such a sequence *paloviridis* holds an intermediate position except for its greatly elongate aedeagus and bursa. One of the geographic variants of *paloviridis* (at Guamúchil) also possesses flattened ventral lobes of the sheath which could easily be the primitive condition in the entire group. However, derivation of other members of the Psolus Group from *paloviridis* requires convergent development of the primitive brown color, shortening of the aedeagus and the opening again of the phallotreme in *contilus.*

The evolution of the *contilus* ancestor from a *cochisei*-like form must have involved the elongation of the dorsal and ventral valves, the ventral lobes of the sheath, and the bursa of the female, as well as the narrowing of the ventral valves, and the development of the distinctive pronotal markings and black femoral stripe. It is no easier to envision ancestral *paloviridis* accomplishing these changes than ancestral *contilus,* except that the development of the color pattern typical of other members of the Psolus Group would have been postponed. On the other hand *paloviridis* must have developed a green ground color, which would subsequently have had to revert to brown at the time it gave rise to the other members of the group.

If *contilus* is accepted as the least changed from the ancestor of the Psolus Group, then the other three members could have developed from it by the elongation of the aedeagus and closure of the phallotreme. The striking similarity of the bursa of *contilus tectatus* to that of *psolus* (see Table 7, p. 38) suggests an ancestral-descendant relationship. The only slightly less similar bursa of *nigrofasciatus,* and the greater similarity of its dorsal valves to those of *tectatus,* suggest a similar relationship. The present distribution of the three species gives evidence of an original inland (foothills)-coastal split of the ancestral *contilus* population. The inland populations developed elongate aedeagi and bursae and closed phallotremes, which was followed by north-south separation leading to the development of modern *psolus* and *nigrofasciatus.* Each of those species has retained different characteristics of the ancestral *contilus tectatus.* We suspect that *paloviridis* evolved from the *psolus-nigrofasciatus* stock. There seems little question

that the characteristics of the populations north of Culiacán where it overlaps with *psolus* are derivative and were developed as a barrier to insemination of *psolus* females (see under Geographic Variation of *paloviridis* and the section on Mechanical Isolation). The sculpturing of the ventral valves of *paloviridis* populations south of Culiacán is very much like that of *psolus* and may indicate a derivation from that species. The dorsal valves in this region (but also in the Guamúchil-Navojoa region to the north) are quite similar to those in *nigrofasciatus,* suggesting a relationship with that species. It is in this southern area also that the hind femora have dark stripes as in the other three members of the Psolus Group. Both *psolus* and *nigrofasciatus* are found at higher altitudes than *paloviridis* and at least *nigrofasciatus* farther inland as well. Thus ancestral *paloviridis* may have developed from a reinvasion of the southern coastal plain from a *psolus-nigrofasciatus* stock. It may have become so successful there that it has replaced *contilus* and *psolus* in all but thorn forest habitats where it seems to be at a disadvantage (see under Habitat of *paloviridis, psolus,* and particularly *contilus tectatus*). Another suggestion of its southern origin is its sympatry with *psolus* north of Culiacán, as opposed to its possible replacement of lowland *psolus* in the Cosalá region, and its infrequent occurrence north of Guamúchil. It may be limited in its southern distribution by *poecilus* which is also abundant in the lowlands south of the Cosalá road. Here it may be outcompeted by an equally well-adapted lowland species. It is also possible that *poecilus* has been spreading northward and invading the range of *paloviridis* and replacing it, possibly through competitive or reproductive exclusion. South of the Cosalá road our records of *paloviridis* are quite infrequent, and may represent relict populations. To better hypothesize on the origin of *paloviridis* we need better data on primitive and derivative similarities, and more distributional data from the foothills of the Sierra Madre.

The success of *paloviridis* in the lowlands may have affected the variation in the bursae of other members of the Psolus Group. If the bursa of *paloviridis* is considered primitive, then selective pressures caused by that species for reproductive isolation might have been responsible for the ventral and subdistal orifice of the thick tube in *psolus* and *contilus,* although the orifice is also ventral in *nigrofasciatus* which is largely allo-

patric to *paloviridis.*

If *contilus* developed in the lowlands where it is now found, then the reinvasion of the lowlands by *paloviridis* and its adaptation to more open environments may be responsible for the present isolation of the subspecies of *contilus.* Populations of *contilus* formerly occupying marginal open habitats may have been eliminated by *paloviridis.* However, the destruction of the thorn forest habitat of *contilus* by man is more likely to have caused both the restriction of *contilus* and the spread of *paloviridis.* This destruction seems to have been too recent a phenomenon to explain the differences among the *contilus* populations. For the original isolation, therefore, one is forced to consider *paloviridis* competition or geographic barriers. Rivers appear to be the only obvious barriers in the latter category. Two of the subspecies come close to, but do not cross rivers (*dicranatus* at the Río San Lorenzo and *contilus* at the Río Humaya) but the ranges of most end far from any major rivers. The present distribution of the *contilus* subspecies is undoubtedly the result of a combination of the several factors discussed above, and we cannot now reconstruct the original isolating factor.

A major stumbling block in any phylogeny of species of *Barytettix* is the distribution of color and color patterns among the species. We have suggested above that brown may be the primitive color in *Barytettix* because it is the commonest color among North American melanoplines even in humid areas with greater quantities of green vegetation. However, this assumption required the independent development of the derivative green color three times no matter which of the above phylogenetic alternatives is chosen (Crassus Group, middle populations of *humphreysii,* and *paloviridis*). Furthermore, the species or populations with green ground color are identical in color pattern (with a few small differences in *terminalis*). If for the sake of argument the assumption is made that green is primitive, other problems are encountered. Although the Crassus Group retains the primitive color (assuming that it represents the descendants of the ancestral species of *Barytettix*), *cochisei* and *contilus,* considered on morphological grounds to be the primitive members of their respective groups, not only possess the derivative color, but also give rise to species with the primitive green color, *humphreysii* (southern populations) and *paloviridis.* The green *humphreysii* populations are unlikely candidates for the ancestor of the Humphreysii Group. They do not retain any particularly primitive features, and a number of reversals would have to be assumed if *humphreysii* were to have given rise to *cochisei* (reduced cerci, blunt, straight ventral valves). Nor is it easier to derive *paloviridis* rather than *contilus* from the Humphreysii or Crassus Groups, and several reversals would also have to have taken place if the other Psolus Group members were to have been derived from *paloviridis* (short aedeagus and bursa and an open phallotreme in *contilus,* as well as independent development of brown ground color).

MECHANICAL ISOLATION

The great interspecific variability of male genitalia in the Melanoplinae has been known since Hubbell (1932) first called attention to it, and since that time this variability has been increasingly important as a taxonomic character. Concomitantly, the biological significance of genitalic variability has probably been assumed to be associated with reproductive isolation. However, evidence for this role has been meager or lacking. It has been known for some time that male genitalic structures in the Oedipodinae and Gomphocerinae show very little interspecific or even intergeneric variability (Gurney, 1940; Barnum, 1959; Uvarov, 1966:388). Otte (1969) demonstrated that, at least in the North American fauna, stridulation in the Gomphocerinae, and wing display and acoustical behavior in the Oedipodinae serve as reproductive isolating mechanisms. In those species of the Melanoplinae which he studied, he found virtually no pre-copulatory behavioral mechanisms of these sorts which might serve that purpose. Thus there appears to be a positive correlation between genitalic variability and degree of development of acoustical behavior or display mechanisms. Considering that the number of mistakes leading to interspecific copulation depends upon the development or excellence of pre-copulatory recognition mechanisms, it may be assumed that errors in recog-

nition would be more common among melano-
pline individuals than between members of
species of the Gomphocerinae and Oedipod-
inae. During the course of the field work carried
out for this study, Cohn found in nature three
examples of mismatings in *Barytettix*. He
estimates that these represent between three and
four percent of the copulations which he ob-
served in the field. Further, in caged individuals
he found that the males and females of different
Barytettix taxa readily accept each other. Such
actual or potential mistakes in interspecific
copulation indicate that there could be selective
pressure on genitalia to serve as isolating mech-
anisms.

We first become interested in the problem of
mechanical isolation in *Barytettix* because we
were intrigued by the enormous differences in
the length of the male aedeagus of members of
the Psolus Group compared with members of
the Humphreysii and Crassus Groups. The ques-
tion of how, in areas of sympatry, the female was
structurally adapted to receive such different
aedeagi under conditions of copulatory error led
Cantrall to study the receptaculum seminis. He
found that the bursa copulatrix was very dif-
ferently developed in the different species
groups. Differences in size, shape, sclerotiza-
tion, and location of the aperture to the thick
tube were striking and, in each group, cor-
related with the basic structure of the terminus
of the male genital mass. Although less pro-
nounced within each group, differences in de-
gree of sclerotization, location of sclerites, and
position of the aperture of the thick tube cor-
related with the shape of the aedeagus and, in
particular, with the opening of the phallotreme.
Details and further consideration of these dif-
ferences are presented by Cantrall and Cohn
(1972)[18].

Based on a comparison of the male aedeagus
and the female bursa copulatrix and thick tube,
we envision several ways in which interspecific

insemination could be *mechanically* prevented in
Barytettix. At least three possibilities are sup-
ported by evidence from our studies. First, it
seems clear that a functional mating is depend-
ent upon the fit, one with the other, of the
aedeagus and the bursa of a mating pair. Any
discrepancy or lack of accommodation in size
and shape of an aedeagus and a bursa is impor-
tant because of the need for the male to elab-
orate and place in position in the female a
spermatophore tube. Gregory (1965) pointed
out that the spermatophore tube is developed
from a fluid produced in the interior of the male
concealed genitalia. This fluid is forced through
the phallotreme and on into the spermathecal
duct of the female. As the fluid passes along
these channels, the outer portions of the cylind-
er of fluid change to form a spermatophore
tube which carries any remaining fluid until the
fluid is exhausted by conversion to sperma-
tophore tube. The male reproductive cells are
then forced through the tube into the diverticu-
lae of the female. Second, the amount of secre-
tion necessary for the production of a sperma-
tophore tube must be dependent upon the area
of the inner surface of the spermathecal duct.
Too large an amount could possibly fill the
diverticulae of the receptaculum seminis thus ex-
cluding spermatozoa, and too little could cause
the length of the spermatophore tube to fall
short of that needed to reach the diverticulae.
Thus a successful mating would be dependent
upon the correct amount of secretion in relation
to the inner surface area of the spermathecal
duct. Third, the need for an alignment of the
opening of the phallotreme with the orifice of
the thick tube seems obvious. If these two open-
ings are not aligned properly the sperma-
tophore tube cannot be threaded into the
spermathecal duct. The locations of the opening
of the phallotreme and of the orifice of the thick
tube relative to the internal genitalia of each of
the members of a mating pair must certainly be
of primary importance to a successful mating.
These three aspects of mechanical isolation are
more amply discussed below as they pertain to
the possible evolutionary development of the
taxa of the genus *Barytettix*.

INTERGROUP MECHANICAL ISOLATION

Owing to differences in size and shape of the
aedeagi and bursae, and of the location of the
opening of the phallotreme and of the thick tube

---

[18]In 1970, at the time of preparation of the manuscript
for this 1973 paper, the present study had not progressed far
enough to enable the naming of the populations discussed
therein. These taxa are now recognizable as:

Cantrall and Cohn, 1972	Present Study
Group A	Humphreysii Group
Group B	Psolus Group
Species 1, Figs. 3, 4, 8, 13	*B. paloviridis*
Species 2, Figs. 9, 14	*B. psolus*
Species 3, Figs. 10, 15	*B. contilus contilus*
Species 4, Fig. 16	*B. nigrofasciatus*
Group C	Crassus Group

it is difficult to envision a successful mating between a female of the Psolus Group and a male of either the Humphreysii or Crassus Groups. The aedeagus of the male is approximately one-fifth the length of the bursa of a female of *paloviridis, psolus,* or *nigrofasciatus* and if inserted into the bursa of one of these species (see particularly Fig. 16; compare Figs. 7, 9, 13, 14 A-H, 17, 18), would leave the distal end of the bursa unoccupied. Even though the aedeagus would fit better in the bursa of a female *contilus,* the discrepancy in lengths would still result in a sac-like space in the bursa. In the absence of a close fit between the opening of the phallotreme and the aperture of the thick tube, the mucilaginous secretion elaborated by the male would pour into this space, preventing the formation of a spermatophore tube capable of conducting spermatodesmes. In a reciprocal mating, the elongate aedeagus of a Psolus Group male (Figs. 13; 14 A-H) would have to penetrate the short bursa of a female of the Humphreysii or Crassus Group (Fig. 16) and hold it in position long enough to produce an effective spermatophore tube. Thus a Psolus Group male would not be able to develop and maintain a proper position to successfully mate with a female from one of the other two groups.

In either of the above crosses a further complication is the location of the aperture of the thick tube as it relates to the distal opening of the phallotreme. In the Crassus and Humphreysii Groups (Figs. 7 B, D, F and 9 B, D, F, respectively) the phallotreme is so formed distally that a developing spermatophore tube is directed disto-dorsally in the bursa (the aedeagus is inserted upside down). The aperture of the thick tube in the females of these two groups is located in the disto-dorsal part of the bursa (Fig. 17 A-F). In the Psolus Group the spermatophore tube is directed disto-ventrally in the bursa except in males of *paloviridis* from the region between the Río Culiacán and the Río San Lorenzo where the opening of the phallotreme is essentially distal. The aperture of the thick tube in the bursa of females of this group is distal, disto-ventral, or ventral. It is evident that a proper alignment between the distal opening of the phallotreme and the opening to the thick tube is not readily obtained in matings between members of the Psolus Group and members of either the Crassus or Humphreysii Groups.

The bursae in members of the Humphreysii and Crassus Groups are not so obviously different in size and shape from one another (Figs. 16 B, E; 17). A major difference is the large dilation found in the proximal end of the thick tube in females of the Crassus Group (Figs. 16 B; 17 A, D). The same area in females of the Humphreysii Group is in no way enlarged (Figs. 16 E; 17 B-C, E-F). We do not yet know the precise manner in which the spermatophore tube is formed in dilations of the thick tube, nor do we know how much spermatophore tube producing fluid a given male can produce during one copulation. If, and we suspect such to be the case, a male is capable of producing only the proper amount of fluid to develop a tube of the correct length in a female of his own species, then, depending upon the members of a mismating, a male might produce too much fluid which could fill and block off the spermatheca, or too little and fail to develop a tube of adequate length to reach the spermatheca.

There is some difference in the size of the aedeagi between members of the Humphreysii and Crassus Groups. Not only are the aedeagi in the Humphreysii Group often twice as long as those found in the Crassus Group, but the widest part is usually almost twice as wide (Figs. 16 B, F). These differences might well have little effect because of the elasticity of the bursal walls which are thinner and less sclerotized than those found in the Psolus Group. On the other hand, the aperture to the thick tube is decidedly dorsal in the bursae of females of the Crassus Group (Fig. 17 D). Further, thickenings exist at this point which we believe have to do with the positioning of the valves of the aedeagus during matings. The valves are bent (Figs. 7 A, C, E) as though they might fit up into the reinforced aperture of the thick tube (Figs. 17 A, D) where they could lock into place ensuring a precise channel through which the spermatophore tube easily could pass. The relationship of the terminus of the aedeagus with the opening to the thick tube is quite different in taxa of the Humphreysii Group (Figs. 9; 16 A-B, E-F; 17 B-C, E-F) where the aperture of the thick tube is more distal and is unreinforced, and the valves of the aedeagi are not down-curved.

Although the question of mechanical reproductive isolation between members of the Crassus and Humphreysii Groups may well be a moot one because the ranges of the two groups

are not known to overlap and they may very well have never been in contact, we believe that genitalic differences between the groups are of sufficient magnitude to preclude crossbreeding were any of the taxa sympatric. The differences in genitalia between members of the Psolus Group and taxa of the Crassus and Humphreysii Groups are much more pronounced. These differences clearly seem to be adequate to function as mechanical reproductive isolating mechanisms for we have no evidence of any intergroup hybridization. Thus it is evident that the three species groups of the genus *Barytettix* have diverged far enough so that mechanical isolation without doubt can function as an intergroup prezygotic isolating mechanism.

INTRAGROUP MECHANICAL ISOLATION

The Humphreysii Group.— Although far more variation is found in the elements of the male genitalia in the Humphreysii Group as compared to the situation in the Crassus Group, the characteristics of the female bursa copulatrix and the thick tube are less well-developed. There are distinct differences between *humphreysii humphreysii* and *humphreysii cochisei* in the shape of the distal portions of the bursa and in the location of the aperture of the thick tube, and smaller but detectable differences in these features between *tridens* and *humphreysii humphreysii*. *Tridens* and *humphreysii humphreysii* are, as presently known, allopatric. In the absence of hybrids or sympatric populations we are unable to judge whether or not the two forms are mechanically isolated. During mating the aciculate processes on the median margin of the dorsal valves in *tridens* (Fig. 9 F) can be expected to deflect dorsally in the bursa a spermatophore tube elaborated by the male. (During copulation the aedeagus is upside-down in the bursa.) This would serve to align the tube with the slightly more proximal aperture to the thick tube found in *tridens*. The more distal aperture to the thick tube and the more distal opening of the phallotreme in *humphreysii* are so located that a spermatophore tube would be directed a little more distally and hybridization between *humphreysii humphreysii* and *tridens* conceivably could be prevented. On the other hand, these differences are minimal and we do have hybrids between *humphreysii humphreysii* and *humphreysii cochisei* where differences in the terminus of the aedeagus and features of the

bursa are much greater. Thus it is possible that the slight differences between *humphreysii humphreysii* and *tridens* are not great enough to prevent hybridization. We have no information on the detailed and precise relationships between the size and shape of the aedeagus, as determined by the morphology of the various aedeagal parts, and the size, shape, degree of sclerotization and location of the sclerites of the walls of the bursa, and the position of the aperture of the thick tube. Neither do we know what effect a mating or several matings may have upon the bursa. What appear to be real and meaningful differences could be the results of stretching and possible distortion from such matings. Dissection of the coupled genitalia of mating pairs should ultimately reveal the fate of the spermatophore tube in matings between individuals of different but closely related taxa. Cantrall is presently working with such material.

The ventral valves of the aedeagus of *humphreysii cochisei* (Figs. 11 A, B) are long and slender, and are close enough to each other to cause the spermatophore tube to issue distally from the phallotreme and prevent it from turning dorsad in the bursa during mating. The orifice of the thick tube is located in the proper position to receive a tube oriented in such a direction (Fig. 17 F). On the other hand, in *humphreysii humphreysii* the ventral valves are of such shape and are oriented in such a manner that the spermatophore tube would need to protrude dorsally (in the bursa) in order to make proper entry into the thick tube. Since we have evidence of hybridization between *humphreysii humphreysii* and *humphreysii cochisei*, the differences in size, shape, and location of the male and female genitalic counterparts seem not to be adequate to produce a completely functional isolating mechanism. However, the number of hybrids which we have found is limited in number, and the areas of hybridization are few and very narrow. The hybrids may have resulted from a chance pairing of two individuals which varied enough from the norm in genitalic structure to enable a transfer of male reproductive cells. If this is what happened, then it is likely that very strong selection for mechanical isolation must be underway between these forms, and reinforcement of this nature could eventually result in the development of completely functional reproductive isolation.

The Crassus Group.— The species of the Crassus Group all have rather similar genitalia. Differences in the bursae found in the three taxa are minor and probably do not represent functional reproductive isolating mechanisms. The species are completely allopatric and there is no apparent evidence of demes of any of the populations having come into contact since isolation. Selection pressure for the evolution of mechanical isolation seems not to have been operative. There is, however, clear evidence in the male aedeagal parts (Fig. 7) of divergence under conditions of isolation. Should demes of differing taxa come into contact in the future, selection pressure would develop for complete mechanical isolation based on differences already present.

The Psolus Group.— Although the close relationship of the members of the Crassus Group foreshadows the development of mechanical isolation as a reproductive isolating mechanism, it is within the Psolus Group that evidence of such developments are most interesting. Here, character reinforcement, as a mechanism for the development of mechanical isolation, is clearly discernible in populations of *paloviridis* which are sympatric with those of *psolus* or with *contilus dicranatus.*

In the area of overlap of the ranges of *paloviridis* and *psolus* the dorsal valves in *paloviridis* almost completely cover the apices of the ventral valves (Fig. 15 P), quite different from the position of these valves in *psolus* (Fig. 15 R). Outside the area of sympatry the ventral valves of *paloviridis* are more extensively exposed, and very similar to *psolus* (compare Fig. 15 Q with R). In these same illustrations a similar pattern is shown in the exposure of the distal opening of the phallotreme. Precisely this same development of the dorsal valves is found where *paloviridis* overlaps the range of *contilus dicranatus.* The aedeagal valves of this subspecies of *contilus* are basically similar to those of *psolus* (Fig. 14 D). Both characters must affect the position or attitude of the spermatophore tube as it emerges from between the dorsal and ventral valves. The tube must find its way into a disto-dorsal aperture of the thick tube in *paloviridis* (Figs. 18 F, L) and a disto-ventral aperture in *psolus* (Figs. 18 D, J) and *dicranatus* (similar to Figs. 18 B, H). In the males of the latter two species the spermatophore tube is able to turn ventrad in the bursa (the aedeagus is inserted upside down into the female) before the apex of the ventral valves because the dorsal valves end much before the apex and the phallotreme is open ventrally in the bursa. In sympatric *paloviridis* the extension of the dorsal valves to the apex of the ventral valves forces the spermatophore tube to emerge straight distally, probably beyond the opening of the ventrally located aperture of the thick tube in *psolus* and *dicranatus.* In this the action of the dorsal valves is aided by the sharp, inward pointing dorso-lateral walls of the phallotreme. In the same manner, the curvature of the ventral valves (Fig. 15 D) also must force the spermatophore tube to emerge disto-dorsally in the bursa and prevent its entry into the ventral aperture in *psolus* and *dicranatus.* Outside the area of sympatry with *psolus* and *dicranatus* the characteristics of each of these structures shift to become more like the condition found in those species. Variation in other aedeagal features in *paloviridis* which undergo character reinforcement in areas of sympatry with *psolus* and *dicranatus* has been discussed in detail above on pages 56-59 and graphed in Figs. 3 and 4. At the moment we can offer little regarding an interpretation of the functions of these features other than to indicate our conviction that they have to do with the proper seating of the aedeagus in the bursa, thus ensuring an alignment of the opening of the phallotreme with the aperture of the thick tube.

Mismatings between *paloviridis* and *psolus* have been observed in the field, yet among the many specimens examined we have not found a single hybrid. In the absence of hybridization we conclude that the differences in genitalic structure account for the failure of mismatings and that these differences represent a mechanical prezygotic isolating mechanism.

The aedeagus and bursa of *nigrofasciatus* are as long as in *psolus* and *paloviridis* (Figs. 14 F-H, N-P; 15 Q; 18 D-F, J-L) and seemingly would make hybridization easy between these species. *Nigrofasciatus* is allopatric with *psolus.* The opening of the phallotreme, the size and shape of the bursa, the location of the aperture of the thick tube, and the pleating and reinforcement of the walls of the bursa are all quite similar between the two species (Figs. 18 D-E, J-K), and are probably not sufficiently different to prevent hybridization if the two forms were sympatric. On the other hand, *nigrofasciatus* and *palo-*

viridis have been taken together at 1.1 mi SW San Ignacio Ferry in Sinaloa. Although 36 specimens of the two species were taken, none show any evidence of hybridization. Since the aedeagi of these species are rather similar (compare Figs. 14 H and 15 Q) the burden of mechanical isolation must fall upon the bursae. These organs are quite different in the two taxa. Not only is the aperture to the thick tube distoventral in *nigrofasciatus* as compared to distodorsal in *paloviridis* (Figs. 18 E-F), but the pleating and reinforcement of the bursal walls is much stronger in *paloviridis* than in *nigrofasciatus* (stippled areas in Figs. 18 K-L). These differences apparently are of sufficient magnitude to serve as a prezygotic isolating mechanism.

In the subspecies of *contilus* selective forces other than those of reproductive isolation must have been responsible for the distinct but uniform differences in the aedeagi (Figs. 14 A-E, I-M). Although these populations are completely allopatric, mechanical isolation has not developed to the point where it is functional, for Cohn in 1970 was able to obtain nymphs from crosses involving *c. tectatus* (Figs. 14 B, J) X *c. dicranatus* (Figs. 14 D, L), and *c. similis* (Figs. 14 E, M) X *c. dicranatus*. Compared with other members of the Psolus Group, the subspecies of *contilus* have a shorter and wider aedeagus (Figs. 14 A-H), the orifice of the thick tube of the receptaculum seminis is ventral, and the thick tube is relatively free of dilation (Fig. 18). It is only in *c. tectatus* that dilation approaching that found in the remaining species of the Psolus Group is present. It is not surprising, therefore, to find that intersubspecific crosses are possible.

Cohn also crossed *c. dicranatus* and *c. tectatus* with both *psolus* and *nigrofasciatus*. As in the crosses above, nymphs were obtained. It is surprising that nymphs were obtained at all, for the aedeagi found in *psolus* and *nigrofasciatus* are longer and narrower than those of the subspecies of *contilus* (Figs. 13 and 14). The bursae of the females reflect in size and shape this same

relationship, and, except for a small dilation in *c. tectatus,* the thick tube dilations in *psolus* and *nigrofasciatus* are not found in *contilus* (Fig. 18). All of the members of the above crosses are allopatric in distribution; the crosses were made in the laboratory and may be considered stress matings.

SUMMARY

Gross interspecific genitalic differentiation has taken place in orthoptera having no or feebly-developed stridulation, wing display, or acoustical behavior. Genitalic divergence in *Barytettix* is strong. Since mismating is not rare in sympatric populations in this genus, it is reasonable to conclude that there is direct selective action on the genitalia as reproductive isolating mechanisms. That this has occurred is indicated by character reinforcement in the genitalia of *paloviridis* where it is sympatric with *psolus* or *contilus dicranatus.* Further, strong bursal differentiation between *paloviridis* and *nigrofasciatus* is evident in a sympatric population of these species. In both of these cases extensive collecting has failed to turn up a single hybrid specimen, although mismatings have been observed between *paloviridis* and *psolus.* Our only hybrids are from areas of subspecific intergradation. In such cases (*humphreysii humphreysii* X *humphreysii cochisei*) the zones of intergradation are narrow, indicating the possibility that genitalic differentiation has developed to a point where it is becoming functional as an isolating mechanism.

In populations of allopatric taxa such as the subspecies of *contilus,* selective action on genitalia seems not to have been adequate to prevent crossing, at least under stress matings in the laboratory. We suggest that under conditions of hybridization in nature resulting from range extension of one or more of these subspecies, character reinforcement with resulting accelerated genitalic differentiation and reproductive isolation will obtain.

PROMISING PROBLEMS

Any intensive taxonomic study will uncover situations of general biological interest. Most often such situations are buried in the body of the resulting paper and readily available only to

taxonomists, and then often only to specialists in a particular group. In this study we have uncovered many problems which seem to have broad evolutionary implications, partly because

we were looking for them, and partly because we have had the time to return to the field to obtain more data on them. In this section we draw together and summarize the problems we have found in *Barytettix*, the discussions of which are scattered through the body of this paper. We do so in the hope of encouraging others to work on them. For the solution of many of these problems, *Barytettix* offers ideal material. The species are usually large, conspicuous and common, and are thus easy to collect. The 1970 work indicates that all taxa can be reared from medium-sized nymphs with little mortality (at least at high temperatures), that all lay eggs readily, and that many eggs hatch without special treatment. Many of the problems reported below are under study by one or the other of us, but there is ample room for others to join us.

Mechanical Isolation.— This is probably the most interesting problem in the genus. Our evidence is indirect that the major prezygotic isolating mechanism in *Barytettix* is genitalic. That there is no pre-copulatory behavioral mechanism still needs to be demonstrated. Although we have three records of mismated couples *in copula* in the field, we have made no study of mating behavior under natural conditions. Cohn conducted two types of cage experiments in 1970. Many combinations of males of one species and females of another always resulted in some copulation. The frequency and length of such copulations, which were not recorded, are probably the critical factors in the efficacy of mechanical isolation. This could readily be compared with conspecific copulations in adjacent cages under almost identical conditions. A second set of experiments involved six males of one species in a cage with six females of their own and six females of another species. At least some of the species appear to copulate at random with the females. The cages were small (slightly less than a cubic foot) and possibly caused the animals trouble with any behavioral mechanism, and no attempt was made to eliminate the possibility of pheromonal attraction. The species of *Barytettix* are easy to handle and observe, and a series of simple experiments could readily be devised to demonstrate the nature of the isolating mechanism.

The only other barrier to insemination between different species is in the misfitting of the genitalia. Our best evidence for this is the aedeagal reinforcement phenomenon in *paloviridis*

where it is sympatric with *psolus* and *contilus dicranatus* in the Culiacán region (see under *paloviridis* Geographic Variation). Further evidence might come from a study of the variability of the aedeagus in *psolus* and *paloviridis* near Cosalá where the two species are largely altitudinally allopatric. Although no reinforcement was seen in either species in the narrow zone of sympatry (see Fig. 3), there appeared to be greater aedeagal variability in the small series of allopatric *psolus* (see under *psolus* Geographic Variation), suggesting a release from strong selective pressure. One of the miscopulating pairs seen in the field was taken in this region. Larger series, more precise determination of range limits, and more frequent collections near those limits in both regions would help to establish this phenomenon more firmly. Less direct evidence for mechanical isolation derives from our comparison of male and female structures in sympatric species. However, all of our ideas concerning the function of the different aedeagal and bursal parts are based on inference (see preceeding section on Mechanical Isolation). Dissection of homo- and heterospecific copulating pairs preserved at different times after the initiation of copulation should demonstrate not only the precise function of each of the parts, but also the significance of aedeagal and bursal differences in preventing insemination. In this, acridologists may have an advantage because the male produces an easily visible, firm, proteinaceous spermatophore tube which must thread into the female spermatheca, a process which apparently takes place over at least an hour's time. Cantrall has begun a study of abdomens from copulating pairs, but it is not yet clear whether the material was adequately preserved. The abdomens were cut from copulating pairs which had been slowly frozen, or from pairs in the field after they had ascended the vegetation in the evening and had become quiescent. In both cases, the abdomens were preserved in alcohol. It may be easier to section preserved copulating abdomens, although the highly sclerotized aedeagal parts may make this difficult. Randell (pers. comm.) may have developed a technique to overcome this difficulty. Gregory (1965:35) reports that abdomens removed from living *Locusta migratoria* continue to function and can be dissected and observed while still alive. This may be a most useful technique in a study of mechanical isolation.

In regard to this problem, it will be of particular interest to know if a copulating male is able to detect a misfit of genitalia, a blockage of the spermatophore tube or an inability to produce enough material for the spermatophore tube (as in the case of a species with a short aedeagus copulating with a female possessing a long bursa, or a male of a species in which the female has an undilated thick tube copulating with a female possessing a dilated thick tube, or vice versa). A male which was able to detect such problems would save much effort. This was suggested by the results of some but not all of the 1970 interspecific laboratory crosses.

If genitalic isolation is proven to be the major mechanism isolating the species of *Barytettix* (and by inference other melanoplines as well), then it would be most interesting to compare the reproductive effort and risks in these species with others in which song and wing display are the primary isolating factors. Superficially it would appear that copulation with any female of the right size and wing shape would be very wasteful of time and energy compared to identification of the right female by some behavioral mechanism prior to copulation. This may not be true, especially in the case of the singing orthoptera in which the males spend long periods of time stridulating. Isolating mechanisms serve two functions in this case, one to attract mates and the other to prevent mismating. It may be that efficient identification is as important as isolation in small dispersed populations, whereas in larger denser populations discrimination is less important and mechanical isolation just as effective. Other factors determining the efficiency of these isolating mechanisms may be density of vegetation, wandering habits, and the abundance of other species. We have made no attempt to correlate any of these factors with the type of isolating mechanism.

Also involved in the problem of the nature and effectiveness of the isolating mechanism are the unusually bright colors in *Barytettix* and the often radically different colors and patterns in the different species. In several cases we have tried to correlate differences in color with sympatry and allopatry. In some cases there is a striking color and pattern difference between sympatric species, as in the sympatry of *paloviridis* with every other member of the Psolus Group. *Contilus, psolus* and *nigrofasciatus* are almost completely allopatric and very similarly colored. However, where *paloviridis* is sympatric with green *humphreysii* the two cannot be told apart by color or color pattern, and where *paloviridis* is sympatric with *poecilus* the species differ only in tibial color. It is interesting to note that just beyond the zone of overlap of the latter two species, *paloviridis* sometimes has purple tibiae just as in *poecilus*. But among other sympatric species there seem to be no clear cases of tibial color being more different there than where the species are allopatric. Tibial color is immensely and strikingly variable between populations as well as between species. It is possible that the bright colors serve merely to attract males to their congeners, and that the actual color makes little difference. This hypothesis agrees with our preliminary findings that some species of caged *Barytettix* do not differentiate between differently colored females. Further cage experiments involving models or painted *Barytettix* might be rewarding.

Finally, the nature of the reproductive isolating or identifying mechanisms may affect the way in which one species is able to penetrate the range of a close relative and thus the nature of the boundary between them. Occasional individuals of a species with only mechanical isolation which invade the range of a relative may spend so much time mating or being mated with the wrong species as to make penetration possible only by large numbers. Even then, the less common species may be quickly eliminated in the zone of overlap by the same mechanism. One might therefore expect related species with only mechanical isolating mechanisms to have contiguous or parapatric ranges (a situation which appears to be common in the Humphreysii and Psolus Groups). Penetration of the range of a relative may be much easier for species with behavioral precopulatory isolating mechanisms. Penetrants of that type will actively seek out an appropriate mate and will ignore and be ignored by the other species. Such species may show more overlapping distributions.

Natural Hybridization.— Only one case of hybridization, as opposed to gradual intergradation, has been found in *Barytettix,* that between *humphreysii humphreysii* and *h. cochisei.* These two taxa were reduced to subspecific status because of our interpretation of two widely separated groups of specimens as hybrids. There appears to be no satisfactory explanation for this hybridization, and the problem is discussed ex-

tensively under *cochisei.* Four intriguing problems are associated with this hybridization.

First, how was insemination accomplished? From a comparison of the male aedeagus and the female bursa it would appear that males of either could not inseminate females of the other species. The elongate ventral valves of *cochisei* would cover the subdistal orifice of the thick tube of *humphreysii,* whereas the subdistally issuing spermatophore tube in *humphreysii* would have difficulty forcing its way past the ventral valves into the distal orifice in *cochisei* (see under Mechanical Isolation). Was the original insemination an accident brought about by a strong difference in size, or by a misshapen aedeagus or bursa? And is subsequent hybridization possible because of the intermediacy of the hybrid genitalia? We have not studied hybrid bursae, and this may hold a clue to the physical mechanism of hybridization.

Second, if the hybridization is not accidental, how have the restricted populations of *cochisei* south of Hermosillo survived without merging with *humphreysii,* or how were they able to intrude into the range of *humphreysii* originally? In this area we have collected only along the main highway; further collections inland may reveal a somewhat different picture. It is hard to believe that the widespread *humphreysii* is at a competitive disadvantage here. However, there is a marked break in the variation of *humphreysii* populations across the area occupied by *cochisei.* This may indicate that there was a gap in the distribution of *humphreysii* there, or that a marked change in some environmental factors occurs in the area, allowing *cochisei* to compete with the edge populations of *humphreysii* which were not so well adapted to the conditions in the gap. But there is also some evidence that *cochisei* was present, but has been eliminated farther south (see discussion under both subspecies).

Third, how is the apparently contiguous distribution of the two taxa maintained in Arizona where there are few obvious barriers? There should either be more evidence of hybridization or examples of sympatry. Our collections in this area are very poor, and transects across the range of the two forms would be very enlightening. Cohn is planning such studies but there is much room for more field work.

Fourth, could a hybrid habitat created by overgrazing or other form of agriculture explain the hybridization between *humphreysii* and *cochisei*? We know little of the ecological requirements of the two. If there was a sharp ecological separation of the two, then a disruption of the habitat where they were contiguous or sympatric may have allowed any accidents in mechanical isolation to survive and contribute further to the breakdown of the isolation between the two taxa. A detailed study of ecological differences between the two species might be relatively easy in this part of Arizona.

Stasipatric Speciation.— Part of White's reason for believing in the widespread occurrence of this form of speciation is the existence of many cases of contiguity or parapatry of closely related species and subspecies rather than their allopatry or sympatry. In *Barytettix* there is one relatively clear case of parapatry of subspecies, that of *h. humphreysii* and *h. cochisei* in Arizona, discussed above. Additional collections have narrowed the gap between the two forms to five to 20 miles at several points along the probable line of contiguity of about 40 miles. No sympatric populations or hybrid swarms have been found. Investigation of the area of contact of the two subspecies in the Hermosillo area might also be rewarding. There however, our collections come only from along the main highway, and the two forms are clearly hybridizing (see under *h. cochisei*). Both areas are of easy access and probably have not been drastically affected by man's activities. We have produced hybrids in the laboratory, but these have not yet matured, and we thus have no data on chromosomal compatibility.

Other cases of suspected contiguity exist among the brown members of the Psolus Group. *Contilus, psolus* and *nigrofasciatus* are all allopatric, as are the five subspecies of *contilus.* However, the ranges of several forms come within a few miles of others especially in the region around Culiacán (see Table 19). This is the area of easiest access in the range of these species, but the region is rapidly being cleared of thorn forest which appears to be their favored habitat. We have no information concerning the breadth of contact between the various forms because our collecting has been restricted to only a few roads. Light plane survey of the road and trail network and of the status of the thorn forest would be easy and would greatly facilitate intensive collecting.

Competitive Exclusion, Reproductive Exclusion, and Habitat Preference.— A number of striking cases of the interruption of the range of one species by another, and the apparent replacement of one by another might be explained readily by one of these phenomena (for the effect of reproductive exclusion see the preceding discussion in this section on Mechanical Isolation). Although we have not specifically sought explanations of such distributional situations, their investigation might be particularly interesting in this genus.

Within the range of the common *h. humphreysii,* small areas occupied exclusively by *paloviridis* are found at 18 mi N Guaymas and just south of that city. *Humphreysii* occupies a number of habitats north and south of Guaymas and is common there (see Table 19). It is thus hard to envision habitat preferences which would exclude *humphreysii* from the areas now occupied by *paloviridis.* However, in Sinaloa there appears to be a distinct difference in habitat preference between *paloviridis* and *tridens,* the southern representative and close relative of *humphreysii.* Whereas in the north *paloviridis* usually occupies only the more moist, bushy habitats, and *humphreysii* the more open, as well as the denser habitats, the reverse is true in Sinaloa. There, *paloviridis* is the occupant of open weedy environments, and *tridens* is the occupant of denser vegetation and thorn forest. Because *tridens* is not common south of Guamúchil, it seems likely that this distributional situation in Sinaloa is the result of habitat preference rather than species interaction.

In a similar manner, *psolus* and *contilus* usually occupy thorn forest or ecotonal habitats and do not venture far into the more open areas occupied by *paloviridis.* In several instances, *paloviridis* was conspicuously absent from habitats occupied by *psolus* and *contilus tectatus* although it was common nearby. Because all three species are often abundant, these situations might be the result of some sort of species interaction. Particularly noteworthy is the absence of *paloviridis* from the weedy summit of Cerro Tule occupied by *contilus tectatus.* Whether *paloviridis,* which is common at the base, cannot penetrate the thorn forest clothing the slopes of the mountain because of physical factors or is being excluded by *tectatus* cannot be determined from the information at hand. The area is ideal for intensive investigation.

On the Cosalá road, *paloviridis* is common in the lowlands but is replaced by *psolus* at around the 700 ft. level; *psolus* becomes equally abundant at higher elevations in and at the edge of thorn forest. The similarity of the habitat of the two species at the edge of the thorn forest leads to the suspicion of interaction between the two.

It is also in this area that *paloviridis* is abruptly replaced by *poecilus* along the main highway (see Table 19). Both species are abundant in roadside weedy, brushy habitats, one to the north and the other to the south of a 10 mile overlap zone. Farther south but several miles inland on the San Ignacio Road, both species are found in a somewhat checkerboard distribution, but are also found together at a few localities.

Near San Ignacio *nigrofasciatus* and *contilus similis* are apparently separated by the Río Piaxtla, but we have not investigated the area thoroughly. The physical barrier of the river and recent arrival in the area of one or both may explain the replacement of one species by the other.

Geographic Variation, Gene Flow and Selection.— Although all *Barytettix* species display some geographic variation, that in *h. humphreysii* and *paloviridis* is unusually extensive and distinctive. A study of gene flow and selection would be facilitated by these factors as well as by the abundance and almost continuous distribution of the two species, and by the well-marked geographic limits of the variants.

Much of the geographic variation in *paloviridis* is associated with the development of mechanical reproductive isolation resulting from interaction with *psolus* and *contilus dicranatus* in Sinaloa (see under Geographic Variation in *paloviridis,* and in the discussion under Mechanical Isolation). Studies of the variation in *paloviridis* characters involved in mechanical isolation near the edge of the range of *psolus* and *dicranatus* (Fig. 3, p. 57, and Fig. 4, p. 59) might yield much information on the swamping phenomenon and the strength of selection. Of particular interest is the striking shift in variation at the Río San Lorenzo. *Paloviridis* occurs commonly on both sides, but *contilus dicranatus* only on the north side.

Almost every character in *h. humphreysii,* from color to concealed genitalia, shows striking geographic variation (see Table 14, p.68). The significance of these variants is unknown.

Many of the changes are abrupt and occur in areas without apparent barriers. Near Hermosillo, at least some of the characteristics in *humphreysii* appear to be the result of introgression from *cochisei*. Near Cd. Obregón a series of concordant changes may be the result of the barrier effect of the Río Yaqui. More collecting needs to be done in this area. Some of the distinctive changes in southernmost Sonora and northernmost Sinaloa seem to be related to the presence of nearby *tridens*. Several of the *humphreysii* characteristics here closely resemble those of *tridens*, while others are more different from *tridens* than are the characteristics of *humphreysii* colonies farther north. These situations are discussed in detail under *h. humphreysii*.

Many of the geographically variable features in *Barytettix* appear only in the adult. Under these circumstances there is the possibility of determining the degree of selective pressures and whether such pressures are sexual or resulting from other environmental factors. The genetic constitution of populations polymorphic for the character under study (such as tibial color in the colonies just north of Imuris) may be determined by rearing a random sample of nymphs to maturity in the laboratory and scoring the adult characteristics. These figures may then be compared with those derived from a random sample collected from the same population several weeks or months after maturity. If sexual selection were operating, a difference might be expected between the frequency of characteristics of the adult population of one year and the preselection frequency (determined by rearing nymphs) of the next year. This situation is probably not as simple as envisioned here, but certainly deserves investigation.

The list of promising problems in this genus, as in any well-studied group of organisms, is endless. We hope that our presentation of several of these problems will encourage others to take advantage of this most interesting genus.

THE DISTRIBUTION OF THE SPECIES OF *BARYTETTIX*

The vast majority of the specimens used in this study were collected along the route of Mexican Highway Number 15, the main west coast highway between the Arizona border at Nogales, and Tepic, Nayarit. Because of the resulting linear distribution we have presented localities in tabular form (Table 19) to illustrate the distribution of the species and subspecies, and to demonstrate more readily problems of overlapping ranges, range limits and gaps in ranges. By utilizing such a list we have been able to include the numbers of specimens collected, which should help in evaluating distributional data relative to allopatric and sympatric species, gaps in ranges, exclusion of one species by another, and similar problems.

We have listed only the records for Sonora, Sinaloa and Chihuahua. The area of contiguity and hybridization of *humphreysii* and *cochisei* in Arizona is mapped in Figure 5, and that in Sonora is treated in Table 17, p. 82 . For areas where only one species occurs, as in Arizona (*humphreysii*), Nayarit and central Jalisco (*poecilus*), southwestern Jalisco (*terminalis*), and Baja California (*crassus*), the presence of the species is indicated in the table by an X, and the records are listed in the species treatment.

Indented localities are those to the east or west of the main highway, and are arranged from north to south and east to west. We have indicated collections containing only females by using the female symbol. All other collections contain at least one male.

We hope that this method of presentation will make the many significant distributional details and problems in *Barytettix* easier to recognize and evaluate, and will enable others who may be interested in working on these problems to complement our collections more effectively.

TABLE 19

DISTRIBUTION OF THE SPECIES OF *BARYTETTIX*

LOCALITIES (distance in miles)	crassus	poecilus	terminalis	c. contilus	c. tectatus	c. hiscatus	c. dicranatus	c. similis	psolus	nigrofasciatus	paloviridis	h. humphreysii	h. cochisei	tridens
CRASSUS GROUP														
PSOLUS GROUP														
HUMPHREYSII GROUP														
ARIZONA – NEW MEXICO														
Southcentral Arizona and Silver City, New Mexico ..	.	.	.	.	.	.	.	.	.	.	.	X	.	.
Southeasternmost Arizona: see Fig. 5, p.	.	.	.	.	.	.	.	.	.	.	.	X	X	.
CHIHUAHUA														
1.8 W Casas Grandes	.	.	.	.	.	.	.	.	.	.	.	18	.	.
SONORA														
7–10 SE Agua Prieta	.	.	.	.	.	.	.	.	.	.	.	.	9	.
Sierra de San José near Naco (hybrids, see text)	.	.	.	.	.	.	.	.	.	.	.	9	.	.
14 road mi SE Cananea	.	.	.	.	.	.	.	.	.	.	.	2	.	.
10 S Cananea	.	.	.	.	.	.	.	.	.	.	.	27	.	.
17.7 N Imuris (31.5 S Nogales, Arizona)	.	.	.	.	.	.	.	.	.	.	.	11	.	.
14 N Imuris	.	.	.	.	.	.	.	.	.	.	.	8	.	.
10.8 N Imuris	.	.	.	.	.	.	.	.	.	.	.	55	.	.
6.1 N Imuris	.	.	.	.	.	.	.	.	.	.	.	18	.	.
3.4 SW Imuris	.	.	.	.	.	.	.	.	.	.	.	10	.	.
5.5 SW Magdalena	.	.	.	.	.	.	.	.	.	.	.	14	.	.
37.2 W Santa Ana	.	.	.	.	.	.	.	.	.	.	.	9	.	.
12 SW Magdalena	.	.	.	.	.	.	.	.	.	.	.	2♀	.	.
14.6 S Santa Ana (1.6 S Llano)	.	.	.	.	.	.	.	.	.	.	.	7	.	.
15.7 S Santa Ana	.	.	.	.	.	.	.	.	.	.	.	3♀	.	.
27.4 S Santa Ana	.	.	.	.	.	.	.	.	.	.	.	21	.	.
39 SSW Magdalena (28 S Santa Ana)	.	.	.	.	.	.	.	.	.	.	.	6	.	.
75 N Hermosillo (Conejos Pass) (32 S Santa Ana) . .	.	.	.	.	.	.	.	.	.	.	.	4	.	.
40.7 S Santa Ana	.	.	.	.	.	.	.	.	.	.	.	5	.	.
50 S Santa Ana (11.3 N El Oasis) (56 N Hermosillo)	.	.	.	.	.	.	.	.	.	.	.	11	.	.
32 N Hermosillo	.	.	.	.	.	.	.	.	.	.	.	3	.	.
Copete Mine, 30 E Carbó (ANSP)	.	.	.	.	.	.	.	.	.	.	.	5♀	.	.
14.2 N Hermosillo Cathedral	.	.	.	.	.	.	.	.	.	.	.	16	.	.
Hermosillo to 48 S (11 S Los Pocitos) (35.5 N Guaymas Cathedral): see Table 5, p.	.	.	.	.	.	.	.	.	.	.	.	X	X	.
18 N Guaymas Cathedral, Puente Noche Buena (28.5 S Los Pocitos, 65.9 S Hermosillo Cathedral) .	.	.	.	.	.	.	.	.	.	.	26	.	.	.
5 NW Guaymas (1 SE jct. San Carlos Road)	.	.	.	.	.	.	.	.	.	.	.	3	.	.
4.2 N Guaymas	.	.	.	.	.	.	.	.	.	.	.	4	.	.
Saladita Bay (4 W Guaymas)	.	.	.	.	.	.	.	.	.	.	.	8	.	.
8 SE Guaymas (6.4 NW Cruz de Piedra)	.	.	.	.	.	.	.	.	.	.	4	.	.	.
10 SE Guaymas (2.6 NW Cruz de Piedra)	.	.	.	.	.	.	.	.	.	.	4	.	.	.

TABLE 19 — DISTRIBUTION OF THE SPECIES OF *BARYTETTIX*

LOCALITIES (distance in miles)	CRASSUS GROUP			PSOLUS GROUP								HUMPHREYSII GROUP		
	crassus	*poecilus*	*terminalis*	*c. contilus*	*c. tectatus*	*c. hiscatus*	*c. dicranatus*	*c. similis*	*psolus*	*nigrofasciatus*	*paloviridis*	*h. humphreysii*	*h. cochisei*	*tridens*
16 SE Guaymas (2.5 SE Cruz de Piedra)	.	.	.	.	.	.	.	.	.	.	4	.	.	.
[17 SE Guaymas, 3 SE Cruz de Piedra — data possibly in error, see T. J. Cohn Field Notebook, 1968, No. 62]	.	.	.	.	.	.	.	.	.	.	.	[4]	.	.
21 SE Guaymas (7–7.3 SE Cruz de Piedra)	.	.	.	.	.	.	.	.	.	.	5	.	.	.
22.7 SE Guaymas (8.6 SE Cruz de Piedra)	.	.	.	.	.	.	.	.	.	.	.	10	.	.
33 SE Guaymas	.	.	.	.	.	.	.	.	.	.	.	2	.	.
37 SE Guaymas	.	.	.	.	.	.	.	.	.	.	.	11	.	.
38.4 SE Guaymas (24.3 SE Cruz de Piedra)	.	.	.	.	.	.	.	.	.	.	.	4	.	.
25 WNW Cd. Obregón (53 SE Guaymas)	.	.	.	.	.	.	.	.	.	.	.	1	.	.
10 NW Cd. Obregón (3.5 W Esperanza)	.	.	.	.	.	.	.	.	.	.	.	5	.	.
Tezopaco (40 road mi NE Esperanza)	.	.	.	.	.	.	.	.	.	.	.	2	.	.
24.7 NE Esperanza (Tezopaco Rd.)	.	.	.	.	.	.	.	.	.	.	.	10	.	.
10 S Cd. Obregón	.	.	.	.	.	.	.	.	.	.	.	2	.	.
22 NW Navojoa (2.9 SE Fundición)	.	.	.	.	.	.	.	.	.	.	.	14	.	.
21 SE Obregón (20.5 NW Navojoa)	.	.	.	.	.	.	.	.	.	.	.	7	.	.
6.8 NW Navojoa	.	.	.	.	.	.	.	.	.	.	.	4	.	.
33.5 road mi NE Alamos Cemetery	.	.	.	.	.	.	.	.	.	.	.	7	.	.
27.4 road mi NE Alamos Cemetery	.	.	.	.	.	.	.	.	.	.	.	7	.	.
19.0 road mi NE Alamos Cemetery	.	.	.	.	.	.	.	.	.	.	.	3	.	.
8.3 road mi NE Alamos Cemetery	.	.	.	.	.	.	.	.	.	.	.	5	.	.
1 S (SE?) Alamos Cemetery	.	.	.	.	.	.	.	.	.	.	.	10	.	.
1 NW Alamos	.	.	.	.	.	.	.	.	.	.	.	14	.	.
2 NW Alamos Cathedral	.	.	.	.	.	.	.	.	.	.	.	10	.	.
13 W Alamos	.	.	.	.	.	.	.	.	.	.	.	13	.	.
10 E Navojoa (23 W Alamos) (Cerro Prieto) . .	.	.	.	.	.	.	.	.	.	.	.	36	.	.
10.4 SE Navojoa	.	.	.	.	.	.	.	.	.	.	.	9	.	.
14.9 SE Navojoa (1.5 SE Bacabachi)	.	.	.	.	.	.	.	.	.	.	.	15	.	.
16.4 SE Navojoa (2.9 SE Bacabachi)	.	.	.	.	.	.	.	.	.	.	.	7	.	.
20.2–21 SE Navojoa (7.4–7.8 SE Bacabachi)	.	.	.	.	.	.	.	.	.	.	.	19	.	.
36.4 SE Navojoa (23.6 SE Bacabachi) (3.2 NW Estación Luis)	.	.	.	.	.	.	.	.	.	.	.	17	.	.
40 SE Navojoa (0.5 SE Estación Luis) (12.1 NW Estación Don) (males only, 13 females not identified to species)	.	.	.	.	.	.	.	.	.	.	6	4	.	.
49.3 SE Navojoa (4.2 NW Estación Don)	.	.	.	.	.	.	.	.	.	.	6	.	.	.
51.8 SE Navojoa (1.7 NW Estación Don)	.	.	.	.	.	.	.	.	.	.	.	10	.	.
SINALOA														
4.4 S Estación Don	.	.	.	.	.	.	.	.	.	.	.	? 1?	.	.
29.2 N Los Mochis turnoff (16.8 S Estación Don) . .	.	.	.	.	.	.	.	.	.	.	2	.	.	.

TABLE 19 – DISTRIBUTION OF THE SPECIES OF *BARYTETTIX*

LOCALITIES (distance in miles)	CRASSUS GROUP			PSOLUS GROUP								HUMPHREYSII GROUP		
	crassus	*poecilus*	*terminalis*	*c. contilus*	*c. tectatus*	*c. hiscatus*	*c. dicranatus*	*c. similis*	*psolus*	*nigrofasciatus*	*paloviridis*	*h. humphreysii*	*h. cochisei*	*tridens*
Cerro Prieto, 23.3 N Los Mochis turnoff (21.3 S Estación Don)	.	.	.	.	.	.	.	.	.	.	.	13	.	.
2.1 S Cerro Prieto, 21.2 N Los Mochis turnoff	.	.	.	.	.	.	.	.	.	.	4	.	.	.
3.4 S Cerro Prieto, 19.9 N Los Mochis turnoff	.	.	.	.	.	.	.	.	.	.	?3♀	.	.	2
3.8 S Cerro Prieto, 19.4 N Los Mochis turnoff	.	.	.	.	.	.	.	.	.	.	5	.	.	.
4.3 S Cerro Prieto, 19.0 N Los Mochis turnoff	.	.	.	.	.	.	.	.	.	.	.	.	.	7
5.3 S Cerro Prieto, 18 N Los Mochis turnoff	.	.	.	.	.	.	.	.	.	.	.	.	.	3
6 S Cerro Prieto, 17.8 N Los Mochis turnoff	.	.	.	.	.	.	.	.	.	.	.	.	.	7
6.2 S Cerro Prieto, 17.1 N Los Mochis turnoff	.	.	.	.	.	.	.	.	.	.	.	.	.	17
12.2 N Los Mochis, 33.6 S Estación Don	.	.	.	.	.	.	.	.	.	.	12	.	.	.
6 NE El Fuerte (52 NE Los Mochis turnoff)	.	.	.	.	.	.	.	.	.	.	.	.	.	17
14 S El Fuerte (32 NE Los Mochis turnoff)	.	.	.	.	.	.	.	.	.	.	.	.	.	9
1.4 SE Los Mochis turnoff	.	.	.	.	.	.	.	.	.	.	.	.	.	3
13.5 W Guamúchil (50 SE Los Mochis turnoff)	.	.	.	.	.	.	.	.	.	.	5	.	.	.
10.9 W Guamúchil	.	.	.	.	.	.	.	.	.	.	13	.	.	17
3.6 W Guamúchil	.	.	.	.	.	.	.	.	.	.	8	.	.	.
62 NW Culiacán Plaza (5 SE Guamúchil)	.	.	.	.	.	.	.	.	5	.	17	.	.	.
60 NW Culiacán Plaza	.	.	.	.	.	.	.	.	5	.	1	.	.	1♀
57 N (NW) Culiacán on Hwy. 15 (ANSP)	.	.	.	.	.	.	.	.	2	.	.	.	.	.
50 NW Culiacán Plaza (3.3 NW Tereros)	.	.	.	.	.	.	.	.	27	.	4	.	.	.
50 NW Culiacán	.	.	.	.	.	.	.	.	4	.	4	.	.	.
5.3 NW Badiraguato (45 WNW Culiacán)	.	.	.	.	.	.	.	.	9	.	.	.	.	.
42 NW Culiacán	.	.	.	.	.	.	.	.	2	.	3	.	.	.
30 N (NW) Culiacán on Hwy. 15 (ANSP)	.	.	.	.	.	.	.	.	.	.	4	.	.	.
20.7 NW Culiacán	.	.	.	.	.	.	.	.	14	.	5	.	.	.
15.2–15.4 NW Culiacán Plaza	.	.	.	.	.	.	.	.	29	.	5	.	.	3
2.5 NW Río Culiacán Bridge at Culiacán (Hwy. 15)	.	.	.	.	.	.	.	.	.	.	43	.	.	.
1–2 E Culiacancito (13 WNW Culiacán)	.	.	.	.	.	.	.	.	.	.	5	.	.	.
2 NW Río Culiacán at Culiacán	.	.	.	.	.	.	.	.	9	.	6	.	.	.
2.5 NW Culiacán Plaza	.	.	.	.	.	.	.	.	.	.	4	.	.	.
6 W Jesús María (19 WNW Culiacán)	.	.	.	.	.	.	.	.	17	.	.	.	.	12
Tecorito–1 W (=La Reforma?) (15 N Culiacán, W side Río Humaya)	.	.	.	.	.	.	.	.	2	.	6	.	.	3
1 E Tecorito (E side Río Humaya)	.	.	.	4	.	.	.	.	.	.	4	.	.	.
1 E San Rafael (W side Río Humaya)	.	.	.	.	.	.	.	.	17	.	1♀	.	.	2
3–3.1 NE Tepuche (13 N Culiacán) (E side Río Humaya)	.	.	.	34	.	.	.	.	.	.	9	.	.	.
± 2 N (NE?) Tepuche	.	.	.	11	.	.	.	.	.	.	6	.	.	.
2.1 NE Tepuche	.	.	.	.	.	.	.	.	?1♀	.	1♀	.	.	.
2 SW Tepuche	.	.	.	.	.	.	.	.	6	.	1	.	.	.
2 W Agua Caliente (9 N Culiacán) (W side Río Humaya)	.	.	.	.	.	.	.	.	7	.	1	.	.	.

TABLE 19 – DISTRIBUTION OF THE SPECIES OF *BARYTETTIX*

LOCALITIES (distance in miles)	CRASSUS GROUP			PSOLUS GROUP								HUMPHREYSII GROUP		
	crassus	*poecilus*	*terminalis*	*c. contilus*	*c. tectatus*	*c. hiscatus*	*c. dicranatus*	*c. similis*	*psolus*	*nigrofasciatus*	*paloviridis*	*h. humphreysii*	*h. cochisei*	*tridens*
Palos Blancos—1 S (8 N Culiacán) (E side Río Humaya)											5			
El Bario (7.5 N Culiacán) (W side Río Humaya)									2		2			
4.7 SW Tepuche (E side Río Humaya)									5		5			
3.9 N Culiacán (E side Río Humaya)											1			
3 NE Culiacán										12	2			
3 N Culiacán (W side Río Humaya)											4			
Culiacán (S end RR. Bridge over Río Culiacán)										16	9			
Culiacán (1 E Cathedral)											30			
2 W Culiacán											2			
15 SW Navolato (27 WSW Culiacán)											7			
Altata, and 1 NE Altata (31 WSW Culiacán)											14			
1.1 W Los Mayos (19.7 road mi ENE Sanalona)							7							
2 W Los Mayos							2				2			
11.4 E Sanalona (30 E Culiacán)							3				2			2
3 E Sanalona							7							
7 E Culiacán (Sanalona Rd.)											8			
±1.5 SE Culiacán											11			
6 SE Culiacán											6			
Cerro Tule Summit (7 SE Culiacán)				7										2
7.2–7.3 SE Culiacán Plaza (Cerro Tule Rd.)				5							14			
9 SE Culiacán				7							10			
13 SE Culiacán											1			
17 SE Culiacán											13			
19.9 SE Culiacán					2						16			
23.9 SE Culiacán							23				5			
30 SE Culiacán (2.4 N Río San Lorenzo)							12				12			
32.7–33 SE Culiacán (S bank Río San Lorenzo)											12			3
35.5 SE Culiacán (3.2 S Río San Lorenzo)											12			
37–38 SE Culiacán											21			
39.9 SE Culiacán											33			
52–53 SE Culiacán											16			
60 SE Culiacán (27 SE Río San Lorenzo)		?6♀									7			
64 SE Culiacán Cathedral (3.1 SE El Espinal)		6						13			2			1♀
66 SE Culiacán		19						7			7			
6.6 E Cosalá (Nuestra Señora Mine Rd.) (60 air mi SE Culiacán), 1600 ft.									9					2
5.6 E Cosalá (Nuestra Señora Mine Rd.), 1500 ft.								12						
2.4 SW Cosalá, 1500 ft.								15						
6 SW Cosalá, 1200 ft								3						

TABLE 19 – DISTRIBUTION OF THE SPECIES OF *BARYTETTIX*

LOCALITIES (distance in miles)	CRASSUS GROUP			PSOLUS GROUP								HUMPHREYSII GROUP		
	crassus	*poecilus*	*terminalis*	*c. contilus*	*c. tectatus*	*c. hiscatus*	*c. dicranatus*	*c. similis*	*psolus*	*nigrofasciatus*	*paloviridis*	*h. humphreysii*	*h. cochisei*	*tridens*
19.5 SW Cosalá, 700 ft	.	.	.	.	.	.	.	.	7	.	6	.	.	3
69.4 SE Culiacán (Cosalá Rd. turnoff), 300 ft	.	3	.	.	.	.	.	.	.	.	10	.	.	.
5.2 NW Río Elota	.	9	.	.	.	.	.	.	.	.	.	.	.	.
4.3 NW Río Elota (40 SE Río San Lorenzo)	.	11	.	.	.	.	.	.	.	.	3	.	.	7
3.5 N Río Elota	.	1♀	.	.	.	.	.	25	.	.	5	.	.	.
63 NW (old) Mazatlán Airport (1.5 NW Río Elota), (77 SE Culiacán)	.	9	.	.	.	.	.	.	.	.	.	.	.	2
58 NW (old) Mazatlán Airport	.	4	.	.	.	.	.	.	.	.	.	.	.	.
84 SE Culiacán (52 N [old] Mazatlán Airport)	.	28	.	.	.	.	.	.	.	.	.	.	.	.
2 N San Ignacio	.	3	.	.	.	.	.	11	.	.	3	.	.	.
1.1 SW San Ignacio Ferry (17.4 NE Coyotitán)	.	13	.	.	.	.	.	.	.	28	8	.	.	.
5.2 NE Coyotitán	.	3	.	.	.	.	.	.	.	.	.	.	.	.
5 NE Coyotitán (49 N [old] Mazatlán Airport)	.	16	.	.	.	.	.	.	.	.	.	.	.	.
48 N (old) Mazatlán Airport	.	18	.	.	.	.	.	.	.	.	.	.	.	.
38.8 N (old) Mazatlán Airport	.	11	.	.	.	.	.	.	.	.	.	.	.	.
29 N (NW) (old) Mazatlán Airport	.	6	.	.	.	.	.	.	.	.	.	.	.	.
31 N Mazatlán on Hwy. 15 (ANSP)	.	.	.	.	.	.	.	.	.	.	1	.	.	.
20 N (old) Mazatlán Airport	.	7	.	.	.	.	.	.	.	.	1	.	.	.
14 N (old) Mazatlán Airport	.	13	.	.	.	.	.	.	.	.	.	.	.	.
El Venadillo (4 N [old] Mazatlán Airport)	.	52	.	.	.	.	.	.	.	.	.	.	.	.
1.3–2.6 NW Villa Unión (W side Río Presidio)	.	5	.	.	.	.	.	.	.	.	.	.	.	.
3.6 NE Santa Lucía (Durango Rd.) (30 NE Concordia)	.	.	.	.	.	.	.	.	.	1♀	.	.	.	.
4 SW Santa Lucía	.	2	.	.	.	.	.	.	.	.	.	.	.	.
8.3 SW Santa Lucía	.	.	.	.	.	.	.	.	.	1	.	.	.	.
12.5 NE Concordia	.	4	.	.	.	.	.	.	.	3	.	.	.	.
11.5 NE Concordia	.	8	.	.	.	.	.	.	.	13	.	.	.	.
4.4–4.6 NE Concordia	.	2	.	.	.	.	.	.	.	3	.	.	.	.
3 NE Concordia	.	6	.	.	.	.	.	.	.	.	.	.	.	.
6.7 SW Concordia	.	3	.	.	.	.	.	.	.	.	.	.	.	.
2–2.4 E Villa Unión (Durango Rd.)	.	15	.	.	.	.	.	.	.	.	.	.	.	.
26 NW Escuinapa	.	5	.	.	.	.	.	.	.	.	.	.	.	.
20 SE Escuinapa	.	3	.	.	.	.	.	.	.	.	.	.	.	.
NAYARIT (See under species account)														
Northwestern and Westcentral Nayarit	.	X	.	.	.	.	.	.	.	.	.	.	.	.
JALISCO (See under species accounts)														
Westcentral Jalisco	.	X	.	.	.	.	.	.	.	.	.	.	.	.
Southwesternmost Jalisco	.	.	X	.	.	.	.	.	.	.	.	.	.	.
TERRITORIO DE BAJA CALIFORNIA (See under species account)														
Southernmost Baja California	X	.	.	.	.	.	.	.	.	.	.	.	.	.

LITERATURE CITED

Ball, E. D., E. R. Tinkham, R. Flock and C. T. Vorhies
1942. The grasshoppers and other Orthoptera of Arizona. Univ. Arizona Agr. Exp. Sta. Tech. Bull. No. 92:254-373.

Barnum, A. H.
1959. The phallic complex in the Oedipodinae (Orthoptera: Acrididae). Ph.D. thesis, Iowa State College. University Microfilms, Inc., Ann Arbor. 220 p.

Berlese, A.
1882. Ricerche sugli organi genitali degli Ortotteri (Mantidae, Locustidae, Gryllidae, Gryllotalpidae, Truxalidae, Acrydiidae). Atti della R. Accad. dei Lincei. Serie terza. Memorie della classe scienze fisiche, matematiche e naturali, 11:259-298.

Bruner, L.
1908. Insecta. Orthoptera. Vol. 11. The Acrididae. Biologia Centrali-Americana. 1902-1909, p. 25-412.

Cantrall, I. J. and T. J. Cohn
1972. Melanoploid genitalia and mechanical isolation. Proc. Intl. Study Conf. Current and Future Problems of Acridology, London, 1970, p. 35-44.

Caudell, A. N.
1908. A New *Barytettix* from Arizona. Proc. Entomol. Soc. Washington 9:69-71.

Cohn, T. J.
1965. The arid-land katydids of the North American genus *Neobarrettia* (Orthoptera: Tettigoniidae): their systematics and a reconstruction of their history. Misc. Publ. Mus. Zool. Univ. Michigan, No. 126:1-179.

Dirsh, V. M.
1956. The phallic complex in Acridoidea (Orthoptera) in relation to taxonomy. Trans. Royal Entomol. Soc. London 108:223-356.

1961. A preliminary revision of the families and sub-families of Acridoidea (Orthoptera: Insecta). Bull. Brit. Mus. (Nat. Hist.), Entomol. 10 (9): 349-419.

Dunbier, R.
1968. The sonoran desert. Its geography, economy and people. Univ. Arizona Press, Tucson. xiii + 426 p.

Fedorov, S. M.
1927. Studies in the copulation and oviposition of *Anacridum aegyptium* L. (Orthoptera: Acrididae). Trans. Entomol. Soc. London 75:53-61.

Gastil, G., R. P. Phillips, R. Rodriquez-Torres, and M. Bonneau
1972. The reconstruction of Mesozoic California. Proc. 24th Intl. Geol. Congr. (Montreal). Section 3:217-229.

Gregory, G. E.
1965. The formation and fate of the spermatophore in the African migratory locust, *Locusta migratoria migratorioides* Reiche and Fairmaire. Trans. Royal Entomol. Soc. London 117 (2):33-66.

Gurney, A. B.
1940. A revision of the grasshoppers of the genus *Orphulella* Giglio-Tos, from America north of Mexico (Orthoptera: Acrididae). Entomologica Amer. 20:85-157.

1951. Revision of the North American grasshoppers of the *Conalcaea* Complex. Proc. U. S. Nat. Mus. 101: 275-304.

Hebard, M.
1917. Notes on Mexican Melanopli (Orthoptera: Acrididae). Proc. Acad. Nat. Sci. Philadelphia 69:251-275.

1925. Dermaptera and Orthoptera from the State of Sinaloa, Mexico, Part II, Saltatorial Orthoptera. Trans. Amer. Entomol. Soc. 51:265-309.

1935. Studies on the Orthoptera of Arizona, Part II, A list of the Dermaptera and Orthoptera with new records and corrections of the literature subsequent to 1909. Trans. Amer. Entomol. Soc. 61:269-316.

Hubbell, T. H.
1932.   A revision of the Puer Group of the North American genus *Melanoplus*, with remarks on the taxonomic value of the concealed male genitalia in the Cyrtacanthacridinae (Orthoptera: Acrididae). Misc. Publ. Mus. Zool. Univ. Michigan, No. 23:1-64.

Kevan, D. K. McE., Syed S. Akbar, and Yu-Cheng Chan
1969.   The concealed copulatory structures of the Pyrgomorphidae (Orthoptera: Acridoidea). Part I. General introduction. Eos 44:165-266.

Key, K. H. L.
1968.   The concept of stasipatric speciation. Systematic Zool. 17:14-22.

Larson, R. L., H. W. Menard, and S. M. Smith
1968.   Gulf of California: a result of ocean-floor spreading and transform faulting. Science 161:781-784.

Mitchell, R. D. and D. R. Cook
1952.   The preservation and mounting of water-mites. Turtox News 30 (9): 4 p.

Nelson, E. W.
1921.   Lower California and its natural resources. Mem. Nat. Acad. Sci. 16 (First Mem.):1-194.

Newell, I. M.
1970.   Construction and use of tabular keys. Pacific Insects 12 (1):25-37.

Otte, D.
1970.   A comparative study of communicative behavior in grasshoppers. Misc. Publ. Mus. Zool. Univ. Michigan, No. 141:1-168.

Packard, A. S.
1878.   Chapter IX. Anatomy and embryology. In: C. V. Riley, A. S. Packard, and C. Thomas. First annual report of the United States Entomological Commission for the Year 1877 relating to the Rocky Mountain Locust, the best methods of preventing its injuries and of guarding against its invasions, in pursuance of an appropriation made by Congress for this purpose. Washington, D. C., p. 257-279.

Paoli, G.
1937.   Osservazioni su alcune particolarita di structtura e funzione dell 'apparato genitale femminile di *Dociostaurus maroccanus* Thnb. (Orthop., Acrididae). Redia 23:17-26.

Randell, R. L.
1963.   On the presence of concealed genitalic structures in female Caelifera (Insecta: Orthoptera). Trans. Amer. Entomol. Soc. 88:247-260.

Rehn, J. A. G. and R. L. Randell
1963.   A preliminary analysis of the lines of the supertribe Melanoplini (Orthoptera: Acrididae: Cyrtacanthacridinae). Proc. Acad. Nat. Sci. Philadelphia 115 (1):1-32.

Rzedowski, J. and R. McVaugh
1966.   La vegetación de Nueva Galicia. Contr. Univ. Michigan Herb. 9 (1): 1-123.

Roberts, H. R.
1941.   A comparative study of the subfamilies of the Acrididae (Orthoptera) primarily on the basis of their phallic structures. Proc. Acad. Nat. Sci. Philadelphia 93:201-246.

Scudder, S. H.
1897a.   The genera of North American Melanopli. Proc. Amer. Acad. Arts and Sciences 32 (9):195-206.

1897b.   Revision of the Orthopteran group Melanopli (Acridiidae), with special reference to North American forms. Proc. U. S. Nat. Mus. 20:1-421.

Slifer, E. H.
1940a.   Variations in the spermatheca of two species of grasshoppers (Orthoptera: Acrididae). Entomol. News. 51:1-3.

1940b.   The internal genitalia of female Ommexechinae and Cyrtacanthacridinae (Orthoptera: Acrididae). J. Morph. 67 (2):199-239.

Thomas, C.
1875.   Report upon the collections of Orthoptera made in portions of Nevada, Utah, California, Colorado, New Mexico and Arizona, during the years 1871, 1872, 1873, and 1874. Rep. Geogr. Geol. Surv. West of the 100th Meridian in charge

of G. M. Wheeler, 5 (Zoology): 843-908 [In: Rep. Geogr. Surv. West of the 100th Meridian]. Washington, D. C.

Uvarov, B. P.
    1966a.   Grasshoppers and locusts. A handbook of general acridology. Vol. 1, Anatomy, physiology, development, phase polymorphism, introduction to taxonomy. Cambridge Univ. Press, London. 481 p.

1966b.   Hibernation of active stages of Acridoidea in temperate climates. Atti della Accademia Gioenia di Scienze Naturali in Catania, Serie Sesta, 18:175-189.

White, M. J. D., R. E. Blackith, R. M. Blackith, and J. Cheney
    1967.   Cytogenetics of the Viatica Group of Morabine grasshoppers. 1. The "Coastal" species. Australian J. Zool. 15:263-302.

Figure 6. Cercus in the species of the genus *Barytettix*. Scale below each figure equals 1 mm.

humphreysii cochisei
    A.   Arizona: Cochise Co., Douglas, W. W. Jones, 1944 (Paratype)
humphreysii humphreysii
    B.   Arizona: Cochise Co., 7 mi N Gleeson, T. J. Cohn, 1951
    C.   Arizona: Pima Co., mouth Madera Canyon, T. J. Cohn, 1957 No. 84
    D.   México: Sonora, 17.7 mi N Imuris, T. J. Cohn, 1965 No. 107
    E.   México: Sonora, 14 mi N Imuris, T. J. Cohn, 1965 No. 106
    F.   México: Sonora, 3.4 mi SW Imuris, T. J. Cohn, 1965 No. 104
    G.   México: Sonora, 5 mi NW Guaymas, T. J. Cohn, 1966 No. 26
    H.   México: Sonora, 33 mi SE Guaymas, T. J. Cohn and E. R. Tinkham, 1957 No. 90
    I.   México: Sonora, 24.7 mi NE Esperanza on Tezopaco Rd., T. J. Cohn, 1966 No. 29
    J.   México: Sonora, 1 mi NW Alamos, T. J. Cohn, 1959 No. 236
    K.   México: Sonora, 21 mi SE Navojoa, T. J. Cohn, 1966 No. 32
tridens
    L.   México: Sinaloa, 6 mi NE El Fuerte, T. J. Cohn, 1966 No. 49
    M.   México: Sinaloa, 17.8 mi N Los Mochis, T. J. Cohn, 1965 No. 93
    N.   México: Sinaloa, 6 mi W Jesús María, T. J. Cohn, 1958 No. 279
    O.   México: Sinaloa, 15 mi N Culiacán, T. J. Cohn and E. R. Tinkham, 1957 No. 106
    P.   México: Sinaloa, 63 mi NW (old) Mazatlán Airport, T. J. Cohn, 1958 No. 257
terminalis
   Q.   México: Jalisco, 16.2 mi NE Barra de Navidad, T. J. Cohn, 1968 No. 33
crassus
    R.   México: Territorio de Baja California, San José del Cabo, ANSP (Topotype)
poecilus
    S.   México: Sinaloa, 66 mi SE Culiacán, T. J. Cohn, 1958 No. 258
    T.   México: Sinaloa, El Venadillo, T. J. Cohn, 1959 No. 214
    U.   México: Sinaloa, El Venadillo, I. J. Cantrall and T. J. Cohn, 1961 No. 55
    V.   México: Sinaloa, 6.7 mi NE Concordia, I. J. Cantrall and T. J. Cohn, 1961 No. 61B
    W.   México: Nayarit, 1 mi W Acaponeta, T. J. Cohn, 1958 No. 303
    X.   México: Nayarit, 8.5 mi SE Acaponeta, I. J. Cantrall and T. J. Cohn, 1961 No. 64
paloviridis
    Y.   México: Sonora, 68 mi S Hermosillo, T. J. Cohn, 1966 No. 24
    Z.   México: Sinaloa, 29.2 mi N Los Mochis (turn off), T. J. Cohn, 1966 No. 35
    AA.   México: Sinaloa, 42 mi NW Culiacán, T. J. Cohn and E. R. Tinkham, 1957 No. 98
    BB.   México: Sinaloa, 1 mi W Tecorito, T. J. Cohn, 1959 No. 221
    CC.   México: Sinaloa, 2.5 mi NW Culiacán, I. J. Cantrall and T. J. Cohn, 1961 No. 56 (Holotype)
nigrofasciatus
    DD.   México: Sinaloa, 8.3 mi SW Santa Lucía, I. J. Cantrall and T. J. Cohn, 1961 No. 52 (Holotype)
psolus
    EE.   México: Sinaloa, 6 mi W Jesús María, T. J. Cohn, 1958 No. 279 (Holotype)
contilus contilus
    FF.   México: Sinaloa, 3 mi NE Tepuche, T. J. Cohn, 1966 No. 40 (Holotype)
contilus tectatus
    GG.   México: Sinaloa, 9 mi SE Culiacán, T. J. Cohn, 1958 No. 288 (Holotype)
contilus hiscatus
    HH.   México: Sinaloa, 19.9 mi SE Culiacán, I. J. Cantrall and T. J. Cohn, 1961 No. 59 (Holotype)
contilus dicranatus
    II.   México: Sinaloa, 30 mi S Culiacán, T. J. Cohn, 1965 No. 85 (Holotype)
continus similis
    JJ.   México: Sinaloa, 66 mi SE Culiacán, T. J. Cohn, 1958 No. 258 (Holotype)

H. COCHISEI

A

H. HUMPHREYSII

B

C

D

E

F

H. HUMPHREYSII

G

H

I

J

K

TRIDENS

L

TRIDENS

M

N

O

P

TERMINALIS

Q

CRASSUS

R

POECILUS

S

T

U

V

W

X

PALOVIRIDIS

Y

Z

AA

BB

CC

NIGROFASCIATUS

DD

PSOLUS

EE

CONTILUS

C. CONTILUS

FF

TECTATUS

GG

C. HISCATUS

HH

C. DICRANATUS

II

SIMILIS

JJ

POECILUS   CRASSUS   TERMINALIS
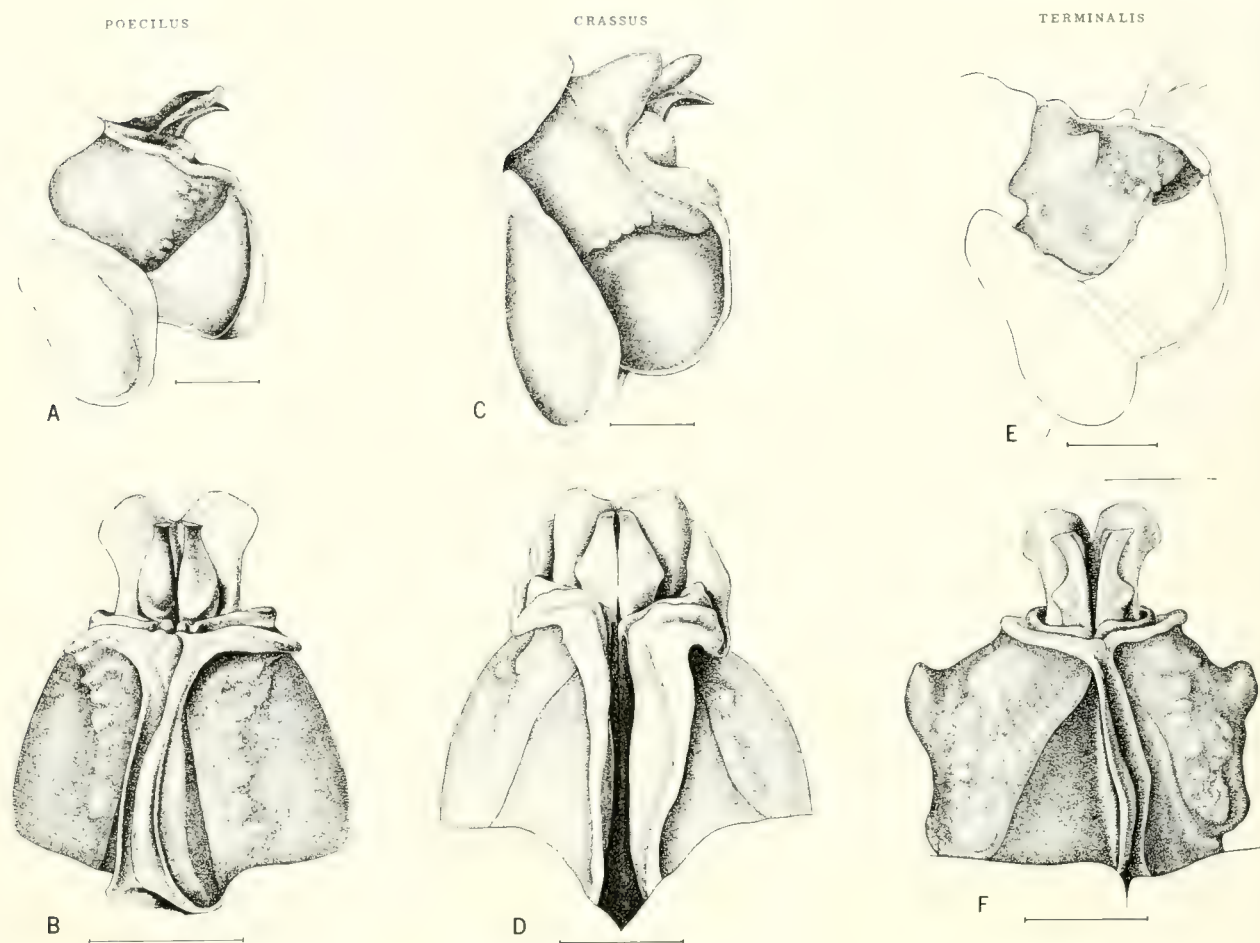
Figure 7. Concealed male genitalia in the Crassus Group of the genus *Barytettix*. Scale below each figure equals 0.5 mm. A, C, E: lateral views. B, D, F: ventral views.

A, B.   *poecilus.* México: Sinaloa, El Venadillo, I. J. Cantrall and T. J. Cohn, 1961 No. 55
C, D.   *crassus.* México: Territorio de Baja California, San José del Cabo (ANSP) (Topotype). In glycerine
E, F.   *terminalis.* México: Jalisco, 16.2 mi NE Barra de Navidad, T. J. Cohn, 1968 No. 33 (Holotype)
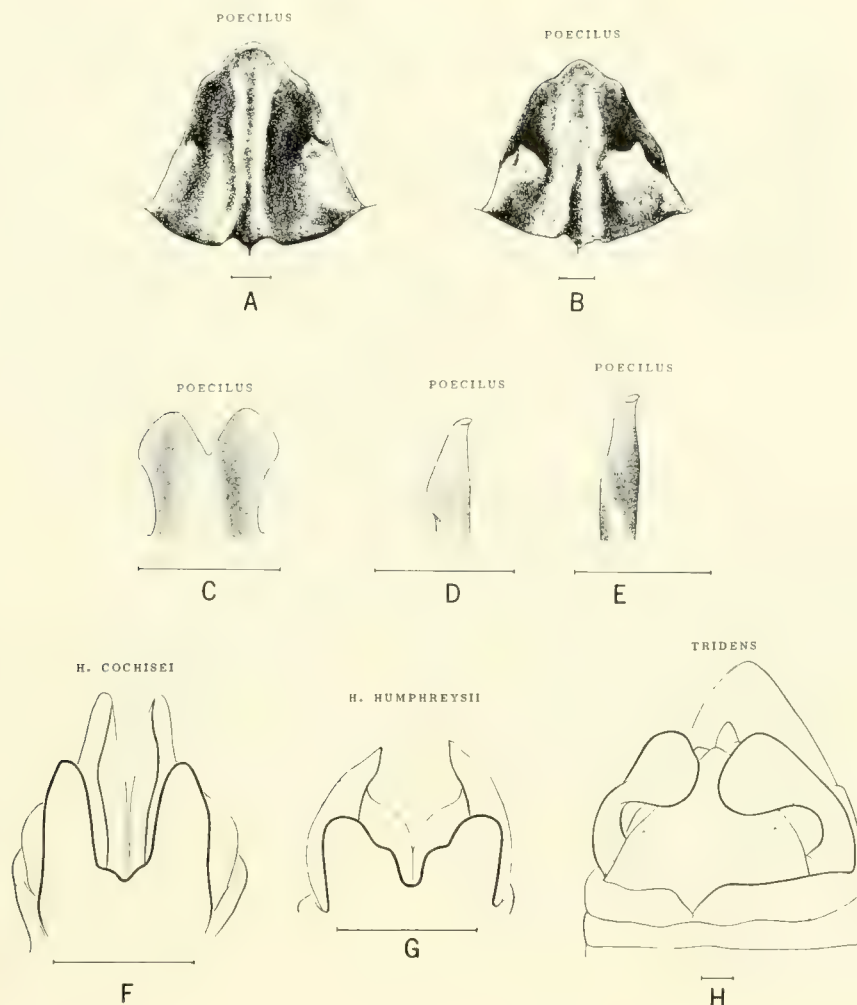
Figure 8.   Genitalic structures and variation in *poecilus* and the Humphreysii Group of the genus *Barytettix*.   Scale below each figure equals 0.5 mm.

A-E. *poecilus*
   A.   Male supra-anal plate. México: Sinaloa, 2.4 mi NE Villa Unión, T. J. Cohn, 1965 No. 82
   B.   Male supra-anal plate. México: Sinaloa, 1.3-2.6 mi NW Villa Unión, T. J. Cohn, 1965 No. 81
   C.   Dorsal valve of aedeagus, dorsal view.   México: Sinaloa, El Venadillo, I. J. Cantrall and T. J. Cohn, 1961 No.55
   D.   Ventral valve of aedeagus, ventral view. México: Sinaloa, 66 mi SE Culiacán, T. J. Cohn, 1961 No. 258
   E.   Ventral valve of aedeagus, ventral view.   México: Jalisco, 5.4 mi E Plan de Barrancas, T. J. Cohn, 1965 No. 73
F-H. Humphreysii Group
   F.   *humphreysii cochisei*.   Dorsal view of aedeagus.   Arizona: Cochise Co., Douglas, W. W. Jones, 1944 (Paratype)
   G   *h. humphreysii*.   Dorsal view of aedeagus. México: Sonora, 37.2 mi W Santa Ana, T. J. Cohn, 1966 No. 51
   H.   *tridens*.   Dorso-lateral view of tip of abdomen. México: Sinaloa, 1 mi W Tecorito, T. J. Cohn, 1959 No. 221

Figure 9.   Concealed male genitalia in the Humphreysii Group of the genus *Barytettix*.   Scale below each figure equals 0.5 mm.   Note: B, D, and F do not include the structures associated with the ramus of the cingulum (as in A, C, and E) and thus are comparable only with the distal portions of Figs. 7 B, D, F and Figs. 13 B, D, F.   Lateral views of genital mass: A, C, E.   Ventral views of aedeagus: B, D, F.

A, B.   *humphreysii humphreysii.* México: Sonora, 17.7 mi N Imuris, T. J. Cohn, 1965 No. 107
C, D.   *humphreysii humphreysii.* México: Sonora, **36** mi SE Guaymas, T. J. Cohn and E. R. Tinkham, 1957 No. 111
E, F.   *tridens.* México: Sinaloa, 63 mi NW (old) Mazatlán Airport, T. J. Cohn, 1958 No. 257

H. HUMPHREYSII

A
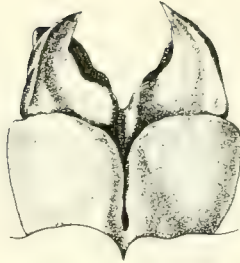
B

H. HUMPHREYSII

C
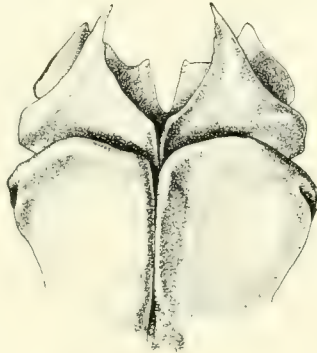
D

TRIDENS

E
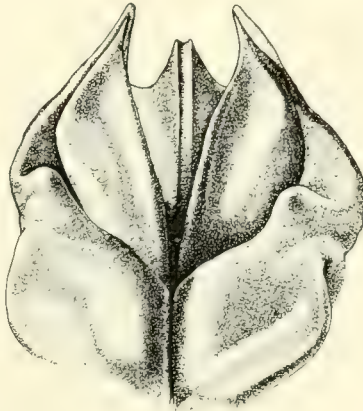
F

Figure 10.   Dorsal valve in dorsal view in the Humphreysii Group of the genus *Barytettix*.   Scale below each figure equals 0.5 mm except for D.

humphreysii cochisei
    A.   New Mexico: Hidalgo Co., 1.5 mi E Rodeo, N. D. Jago, 1968 (ANSP)
    B.   México: Sonora, 7-10 mi SE Agua Prieta, V. Roth, T. J. Cohn and J. W. Cohn, 1970 No. 23
    C.   Arizona: Cochise Co., Douglas, W. W. Jones, 1944 (Paratype)
    D.   Arizona: Cochise Co., Douglas, W. W. Jones, 1944 (Holotype, USNM)
    E.   México: Sonora, 10.4 mi S Hermosillo, T. J. Cohn, 1965 No. 101
humphreysii humphreysii
    F.   Arizona: Cochise Co., 7 mi N Gleeson, T. J. Cohn, 1951
    G.   México: Sonora, 17.7 mi N Imuris, T. J. Cohn, 1965 No. 107
    H.   México: Sonora, 3.4 mi N Imuris, T. J. Cohn, 1965 No. 104
    I.   México: Sonora, 5.5 mi SW Magdalena, T. J. Cohn, 1966 No. 103
    J.   México: Sonora, 14 mi N Hermosillo, T. J. Cohn, 1966 No. 21
    K.   México: Sonora, 4.2 mi N Guaymas, T. J. Cohn, 1959 No. 237
    L.   México: Sonora, 33 mi SE Guaymas, T. J. Cohn and E. R. Tinkham, 1957 No. 90
    M.   México: Sonora, 37 mi SE Guaymas, T. J. Cohn and E. R. Tinkham, 1957 No. 111
    N.   México: Sonora, Tezopaco, F. Pacheco M., 1956
    O.   México: Sonora, 24.7 mi NE Esperanza on Tezopaco Rd., T. J. Cohn, 1966 No. 29
    P.   México: Sonora, 1 mi NW Alamos, T. J. Cohn, 1959 No. 236
    Q.   México: Sonora, 21 mi SE Navojoa, T. J. Cohn, 1966 No. 32
    R.   México: Sonora, 51.8 mi SE Navojoa, T. J. Cohn, 1966 No. 34
tridens
    S.   México: Sinaloa, 6 mi W Jesús María, T. J. Cohn, 1958 No. 279
    T.   México: Sinaloa, 63 mi NW (old) Mazatlán Airport, T. J. Cohn, 1958 No. 257

H. COCHISEI · H. HUMPHREYSII · H. HUMPHREYSII · H. HUMPHREYSII

A · F · K · P

B · G · L · Q

C · H · M · R

D · I · N · TRIDENS S

E · J · O · T
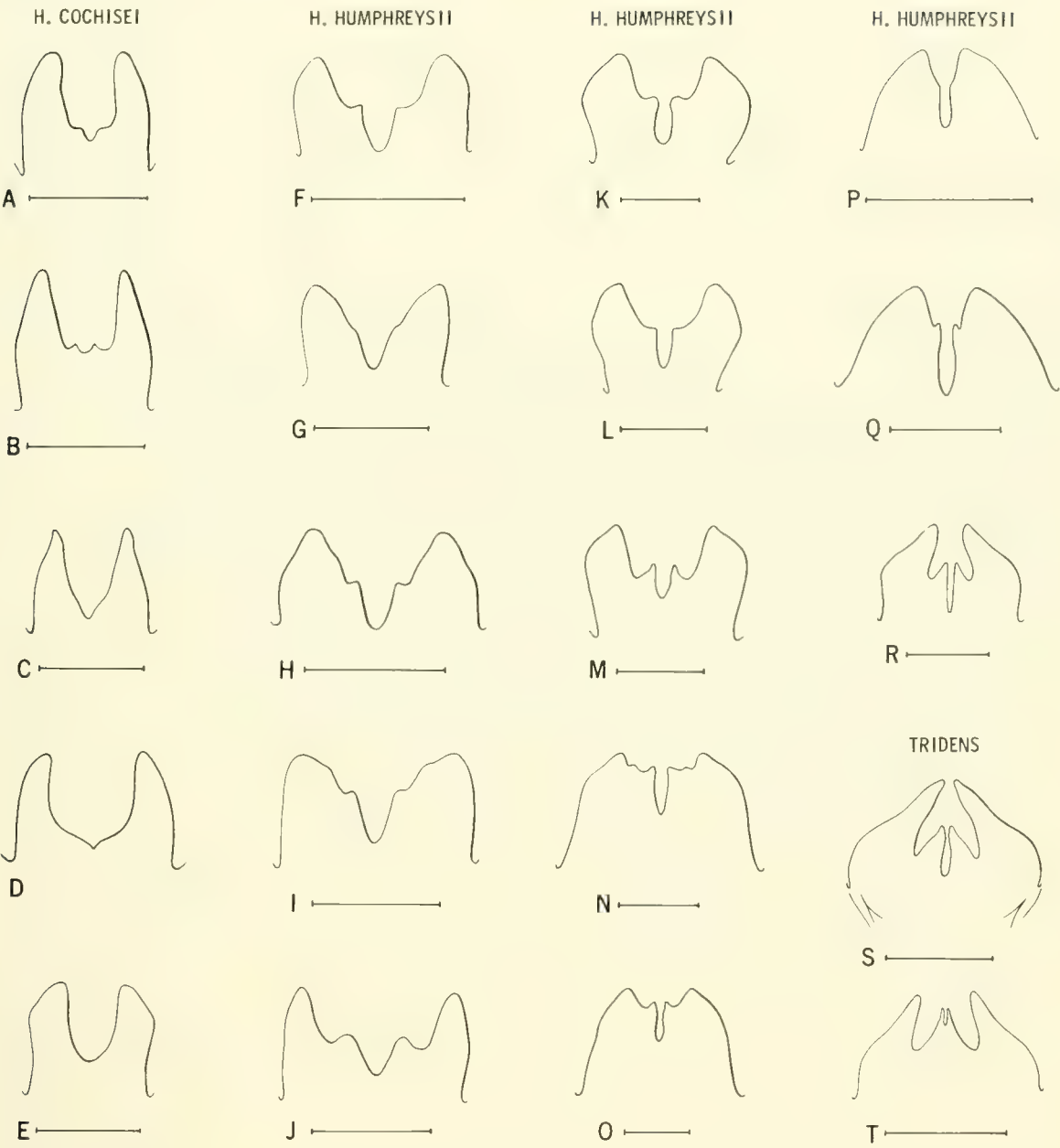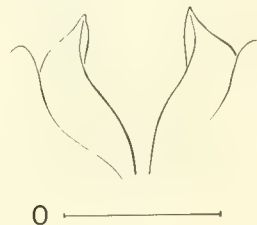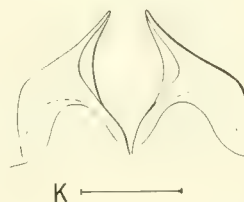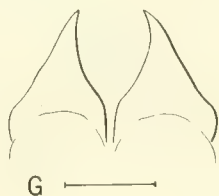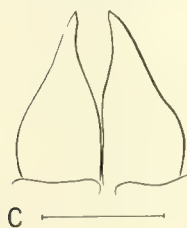
Figure 11. Ventral valves in ventral view in the Humphreysii Group of the genus *Barytettix*. Scale below each figure equals 0.5 mm.

humphreysii cochisei
   A.   Arizona: Cochise Co., Douglas, W. W. Jones, 1944 (Paratype)
   B.   México: Sonora, 10.4 mi S Hermosillo, T. J. Cohn, 1965, No. 101
cochisei-humphreysii hybrids
   C.   Arizona: Cochise Co., Don Luis, Rehn and Hebard, 1922 (*cochisei* paratype) (USNM)
   D.   México: Sonora, 0.7 mi N Los Pocitos (36.8 mi S Hermosillo Cathedral), T. J. and J. W. Cohn, 1970 No. 68
humphreysii humphreysii
   E.   Arizona: Santa Cruz Co., 4 mi E Arivaca, T. J. Cohn, 1951
   F.   Arizona: Pima Co., mouth Madera Canyon, T. J. Cohn and E. R. Tinkham, 1957 No. 84
   G.   México: Sonora, 48 mi S Hermosillo, T. J. Cohn, 1965 No. 99
   H.   México: Sonora, 4.2 mi N Guaymas, T. J. Cohn, 1959 No. 237
   I.   México: Sonora, Tezopaco, F. Pacheco M., 1956
   J.   México: Sonora, 24.7 mi NE Esperanza on Tezopaco Rd., T. J. Cohn, 1966 No. 29
   K.   México: Sonora, 10 mi S Cd. Obregón, F. Orozco, 1957
   L.   México: Sonora, 1 mi NW Alamos, T. J. Cohn, 1959 No. 236
   M.   México: Sonora, 51.8 mi SE Navojoa, T. J. Cohn, 1966 No. 34
tridens
   N.   México: Sinaloa, 6 mi NE El Fuerte, T. J. Cohn, 1966 No. 49
   O.   México: Sinaloa, 17.8 mi N Los Mochis, T. J. Cohn, 1965 No. 93
   P.   México: Sinaloa, 6 mi W Jesús María, T. J. Cohn, 1958 No. 279

H. COCHISEI   H. HUMPHREYSII   H. HUMPHREYSII   H. HUMPHREYSII
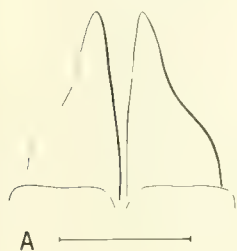
A

B

COCHISEI - HUMPHREYSII
HYBRIDS

C

D

E

F

G

H

I

J

K

L

M

TRIDENS

N

O

P
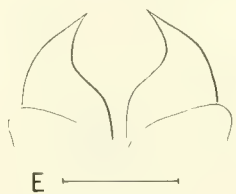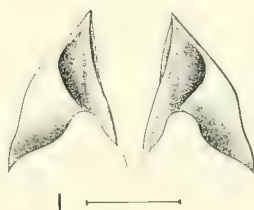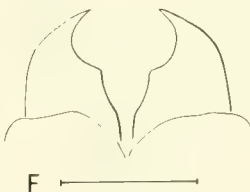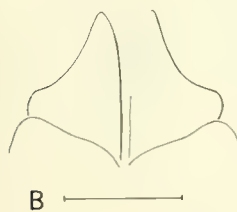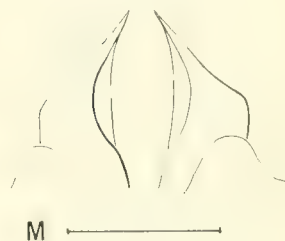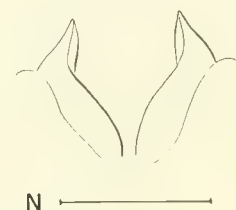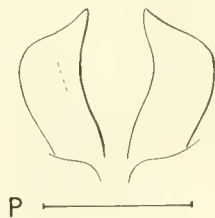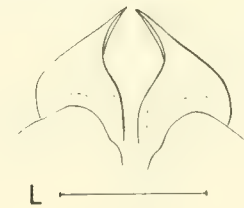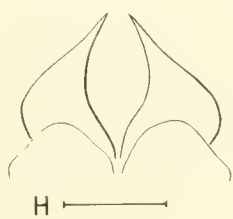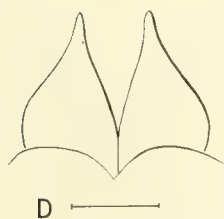
Figure 12. Ventral lobes of the sheath in ventral view in the Humphreysii Group of the genus *Barytettix*.   Scale below each figure equals 0.5 mm.

humphreysii cochisei
    A.   Arizona: Cochise Co., Douglas, W. W. Jones, 1944 (Paratype)
    B.   México: Sonora, 10.4 mi S Hermosillo, T. J. Cohn, 1965 No. 101
humphreysii humphreysii
    C.   Arizona: Pima Co., mouth Madera Canyon, T. J. Cohn and E. R. Tinkham, 1957 No. 84
    D.   México: Sonora, 14 mi N Imuris, T. J. Cohn, 1965 No. 106
    E.   México: Sonora, 37.2 mi W Santa Ana, T. J. Cohn, 1966 No. 51
    F.   México: Sonora, 4.2 mi N Guaymas, T. J. Cohn, 1959 No. 237
    G.   México: Sonora, Tezopaco, F. Pacheco M., 1956
    H.   México: Sonora, 24.7 mi NE Esperanza on Tezopaco Rd., T. J. Cohn, 1966 No. 29
    I.   México: Sonora, 10 mi S Cd. Obregón, F. Orozco, 1957
    J.   México: Sonora, 6.8 mi NW Navojoa, T. J. Cohn, 1965 No. 94
    K.   México: Sonora, 1 mi NW Alamos, T. J. Cohn, 1959 No. 236
    L.   México: Sonora, 21 mi SSE Navojoa, T. J. Cohn and E. R. Tinkham, 1957 No. 95
    M.   México: Sonora, 21 mi SE Navojoa, T. J. Cohn, 1966 No. 32
    N.   México: Sonora, 51.8 mi SE Navojoa, T. J. Cohn, 1966 No. 34
tridens
    O.   México: Sinaloa, 6 mi NE El Fuerte, T. J. Cohn, 1966 No. 49
    P.   México: Sinaloa, 17.8 mi N Los Mochis, T. J. Cohn, 1965 No. 93
    Q.   México: Sinaloa, 15.2 mi NW Culiacán, T. J. Cohn, 1966 No. 43
    R.   México: Sinaloa, 6 mi W Jesús María, T. J. Cohn, 1958 No. 279
    S.   México: Sinaloa, 33 mi SE Culiacán, T. J. Cohn, 1958 No. 260

H. COCHISEI

H. HUMPHREYSII

H. HUMPHREYSII

TRIDENS

A

E

J

O

B

F

K

P

H. HUMPHREYSII

G

L

Q

C

H

M

R

D

I

N

S
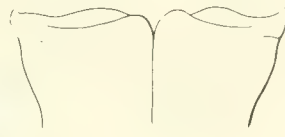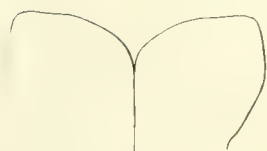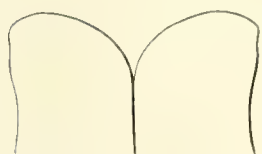
PALOVIRIDIS   PSOLUS   C. HISCATUS
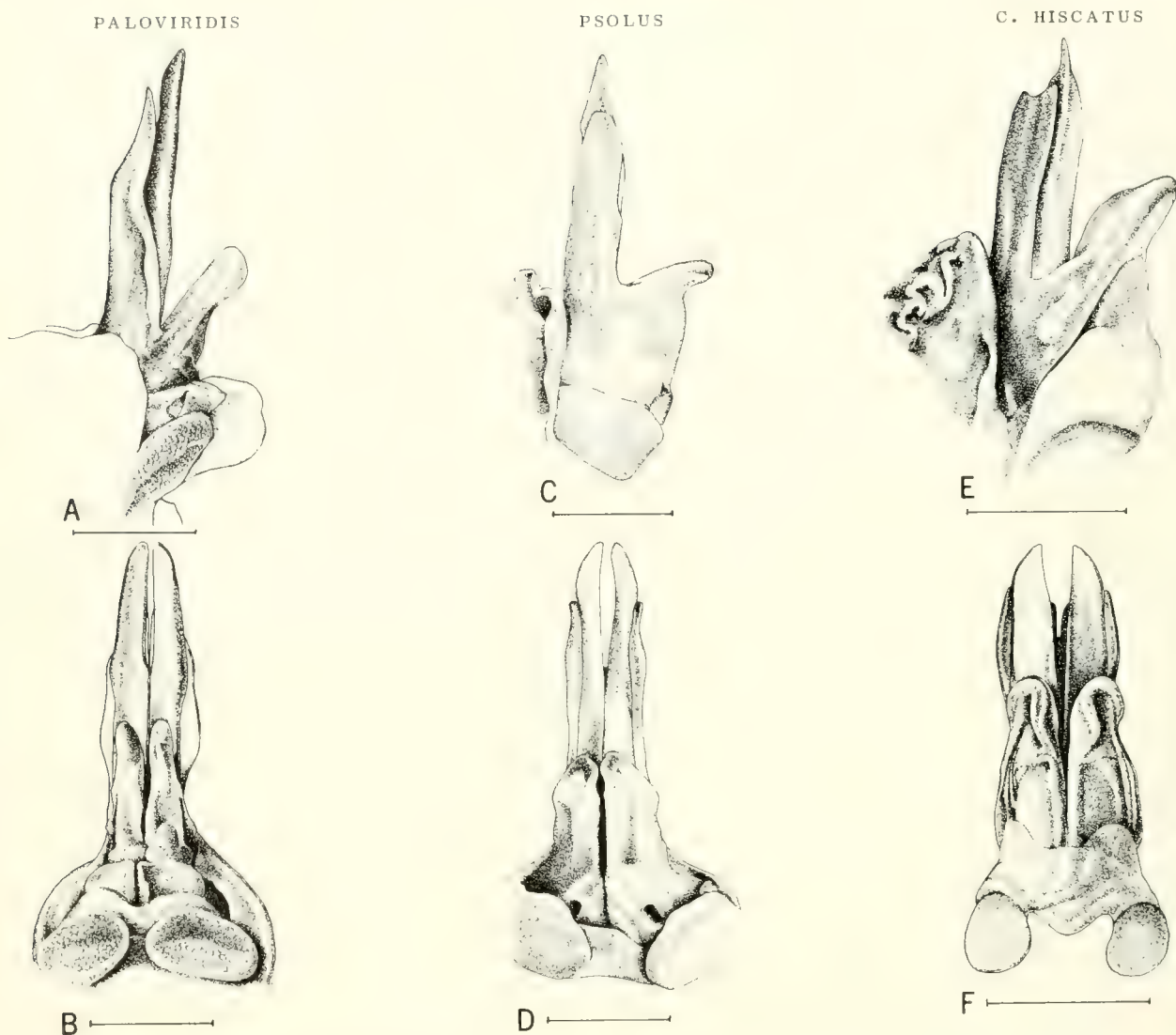

Figure 13. Concealed male genitalia in the Psolus Group of the genus *Barytettix*.   Scale below each figure equals 1 mm. A, C, E: lateral views. B, D, F: ventral views.

A, B.   *paloviridis*. México: Sinaloa, 39.9 mi SE Culiacán, I. J. Cantrall and T. J. Cohn, 1961 No. 60
C, D.   *psolus*. México: Sinaloa, 15 mi N Culiacán, E. R. Tinkham and T. J. Cohn, 1957 No. 106
E, F.   *contilus hiscatus*.   México: Sinaloa, 19.9 mi SE Culiacán, I. J. Cantrall and T. J. Cohn, 1961 No. 59 (Holotype)
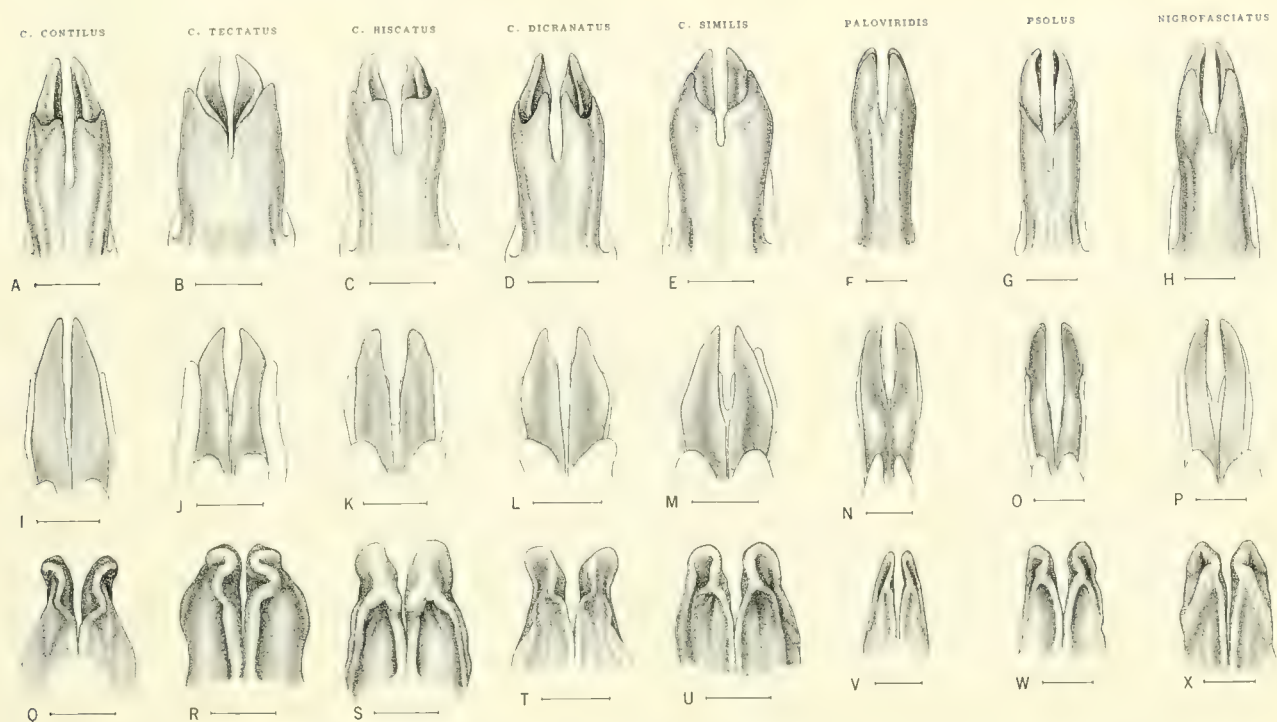
Figure 14. Aedeagal structures in the Psolus Group of the genus *Barytettix*. Scale below each figure equals 0.5 mm. A-H. Dorsal views of aedeagus. I-P: ventral views of aedeagus. Q-X: ventral lobes of sheath, ventral views (as if lobes are closely appressed to ventral valves).

A, I, Q.   *contilus contilus.* México: Sinaloa, 3 mi NE Tepuche, T. J. Cohn, 1966 No. 40 (Holotype)
B, J, R.   *contilus tectatus.* México: Sinaloa, 9 mi SE Culiacán, T. J. Cohn, 1958 No. 288 (Holotype)
C, K, S.   *contilus hiscatus.* México: Sinaloa, 19.9 mi SE Culiacán, I. J. Cantrall and T. J. Cohn, 1961 No. 59 (Holotype)
D, L, T.   *contilus dicranatus.* México: Sinaloa, 30 mi S Culiacán, T. J. Cohn, 1965 No. 85 (Holotype)
E, M, U.   *contilus similis.* México: Sinaloa, 66 mi SE Culiacán, T. J. Cohn, 1958 No. 258 (Holotype)
F, N, V.   *paloviridis.* México: Sinaloa, 2.5 mi NW Culiacán, I. J. Cantrall and T. J. Cohn, 1961 No. 56 (Holotype)
G, O, W.   *psolus.* México: Sinaloa, 6 mi W Jesús María, T. J. Cohn, 1958 No. 279 (Holotype)
H, P, X.   *nigrofasciatus.* México: Sinaloa, 8.3 mi SW Santa Lucía, I. J. Cantrall and T. J. Cohn, 1961 No. 52 (Holotype)
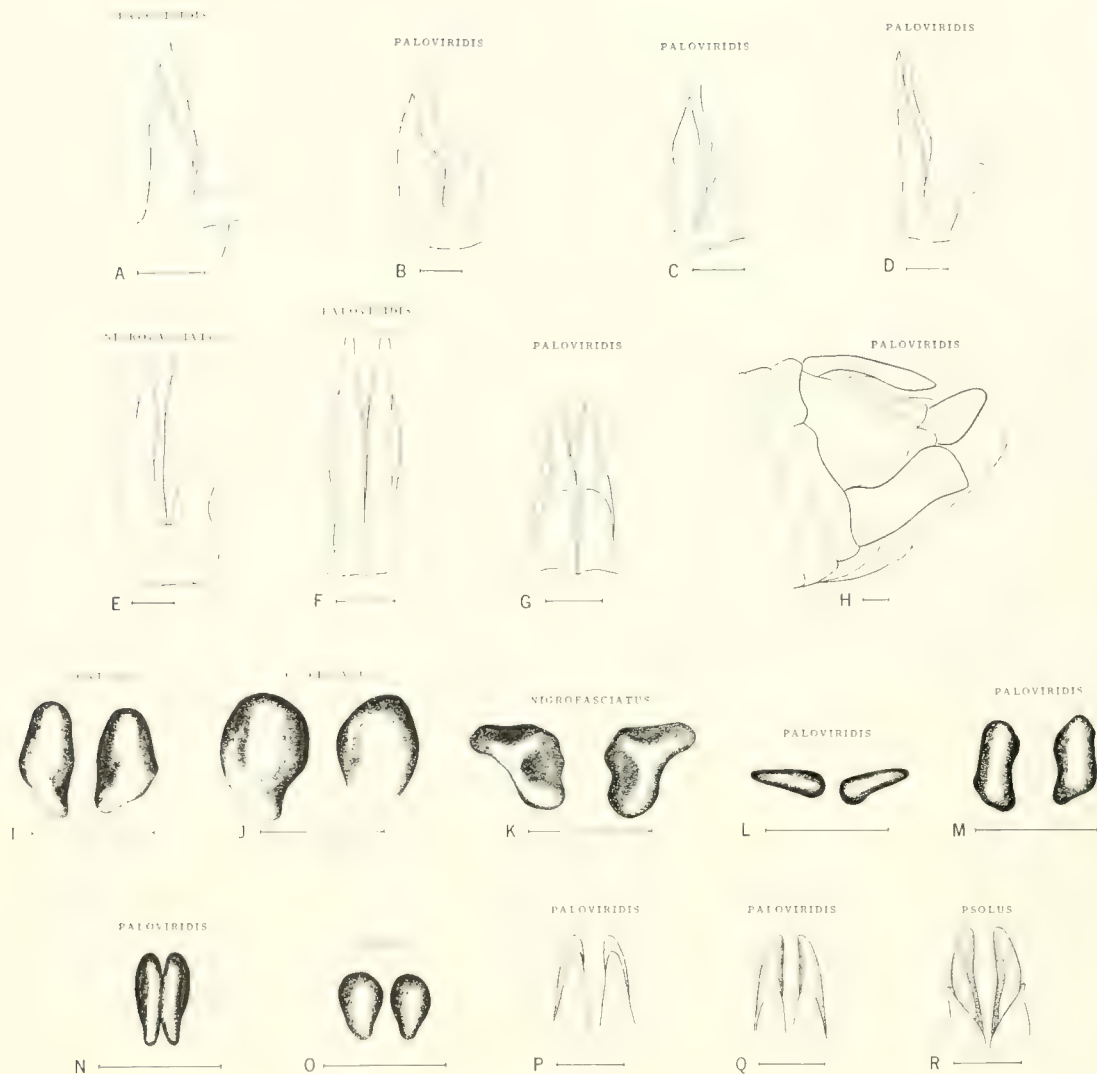
Figure 15. Aedeagal details and tip of abdomen in the Psolus Group of the genus *Barytettix*. Scale below each figure equals 0.5 mm.

A-E.   Side views of aedeagus
    A.   *paloviridis.* México: Sonora, 18.2 mi N Guaymas, T. J. Cohn, 1968 No. 63
    B.   *paloviridis.* México: Sonora, 68 mi S Hermosillo, T. J. Cohn, 1966 No. 24
    C.   *paloviridis.* México: Sinaloa, 3.6 mi W Guamúchil, T. J. Cohn, 1965 No. 90
    D.   *paloviridis.* México: Sinaloa, 2.5 mi NW Culiacán, I. J. Cantrall and T. J. Cohn, 1961 No. 56 (Holotype)
    E.   *nigrofasciatus.* México: Sinaloa, 8.3 mi NW Santa Lucía, I. J. Cantrall and T. J. Cohn, 1961 No. 52 (Holotype)
F-G.   Ventral views of aedeagus in *paloviridis*
    F.   México: Sinaloa, 10.9 mi W Guamúchil, T. J. Cohn, 1968 No. 11
    G.   México: Sinaloa, 3.6 mi W. Guamúchil, T. J. Cohn, 1965 No. 90
H.   Dorso-lateral view of tip of abdomen in *paloviridis*
    H.   México: Sinaloa, 17 mi SE Culiacán, T. J. Cohn, 1958 No. 294
I-O.   Distal views of ventral loves of the sheath
    I.   *contilus contilus.* México: Sinaloa, 3 mi N Tepuche, T. J. Cohn, 1966 No. 40
    J.   *contilus hiscatus.* México: Sinaloa, 19.9 mi SE Culiacán, T. J. Cohn, 1961 No. 59 (Holotype)
    K.   *nigrofasciatus.* México: Sinaloa, 8.3 mi SE Santa Lucía, I. J. Cantrall and T. J. Cohn, 1961 No. 52 (Holotype)
    L.   *paloviridis.* México: Sinaloa, 10.9 mi W Guamúchil, T. J. Cohn, 1968 No. 11
    M.   *paloviridis.* México: Sinaloa, 17 mi SE Culiacán, T. J. Cohn, 1958 No. 294
    N.   *paloviridis.* México: Sinaloa, El Bario, T. J. Cohn, 1959 No. 231
    O.   *psolus.* México: Sinaloa, El Bario, T. J. Cohn, 1959 No. 231
P-R.   Dorsal views of tip of aedeagus
    P.   *paloviridis.* México: Sinaloa, 30 mi S Culiacán, T. J. Cohn, 1965 No. 85
    Q.   *paloviridis.* México: Sinaloa, 33 mi SE Culiacán, T. J. Cohn, 1958 No. 260
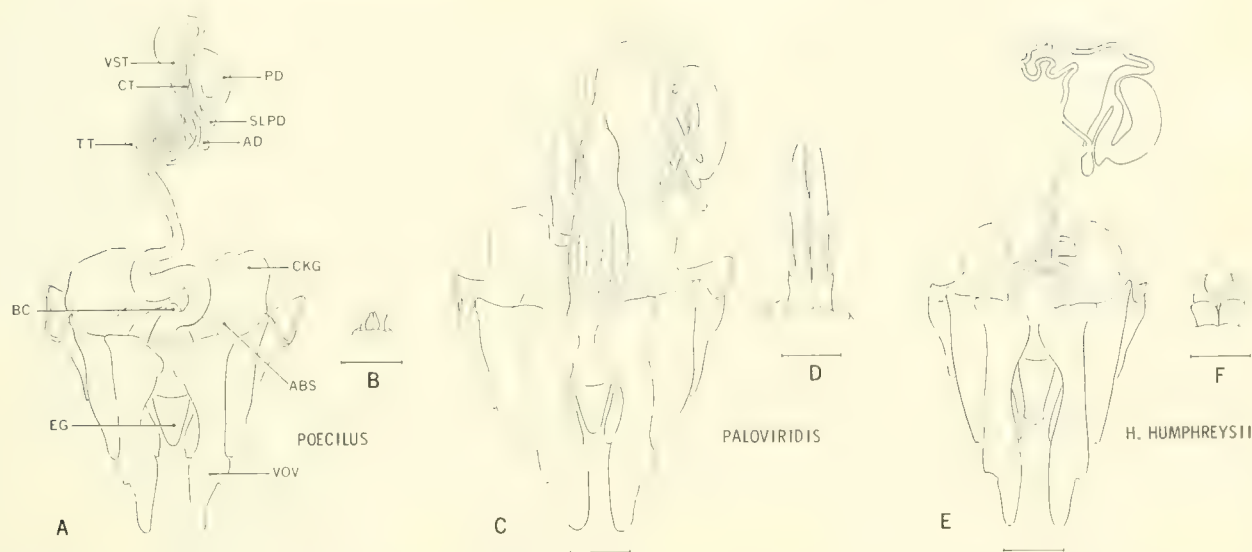   R.   *psolus.* México: Sinaloa, 3 mi NW Culiacán, T. J. Cohn, 1968 No. 267

Figure 16. Ovipositor and receptaculum seminis, and aedeagus of representatives of the groups of *Barytettix*. A, C, E: female structures in dorsal view. Scale below each figure equals 1 mm. B, D, F: male aedeagus in ventral view (as they would be inserted into the female) drawn to the same scale as that of the female structures.

A.   *poecilus*. México: Sinaloa, 84 mi SE Culiacán, T. J. Cohn, 1958 No. 244
B.   *poecilus*. México: Sinaloa, El Venadillo, 4 mi N (old) Mazatlán Airport, I. J. Cantrall and T. J. Cohn, 1961 No. 55 (Topotype)
C.   *paloviridis*. México: Sinaloa, 2.5 mi NW bridge over Río Culiacán at Culiacán, I. J. Cantrall and T. J. Cohn, 1961 No. 56 (Topotype)
D.   *paloviridis*. México: Sinaloa, 39.9 mi SE Culiacán, I. J. Cantrall and T. J. Cohn, 1961 No. 60
E.   *humphreysii humphreysii*. Arizona: Pima Co., Sabino Canyon, Santa Catalina Mts., M. Cazier, P. Boone and T. J. Cohn, 1950
F.   *humphreysii humphreysii*. México: Sonora, 17.7 mi N Imuris, T. J. Cohn, 1965 No. 107

Symbols used in figures:

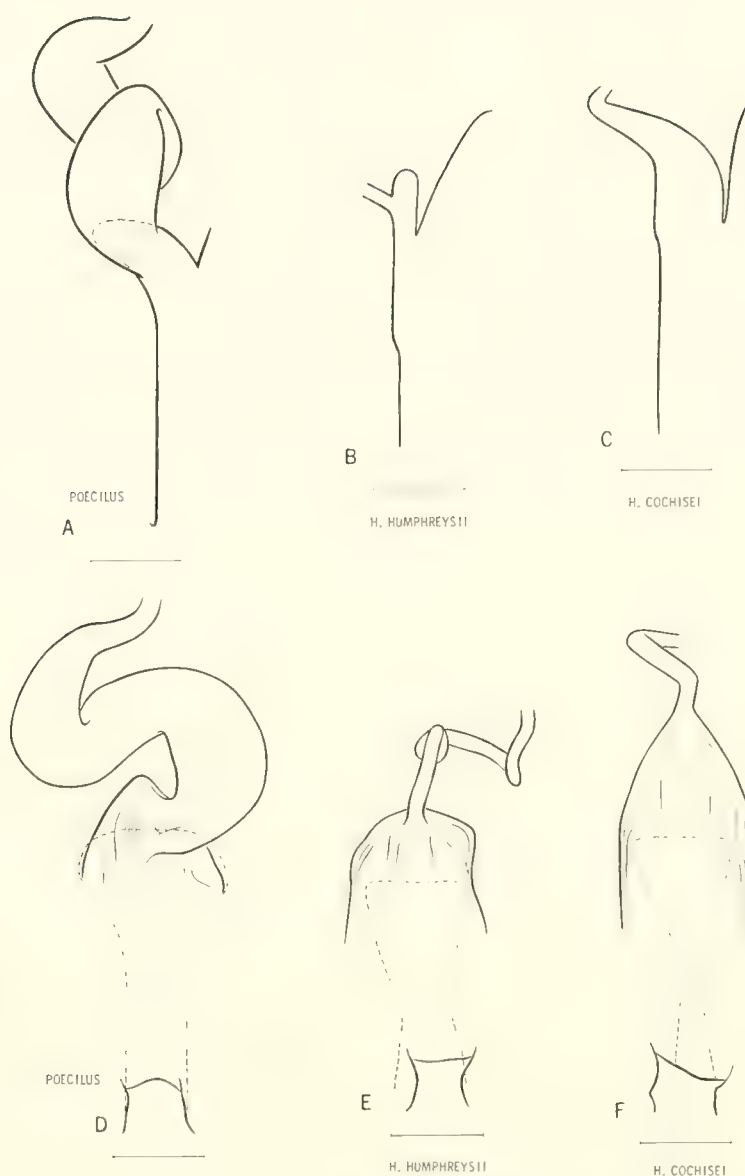|		
ABS	—	anterior basivalvular sclerite
AD	—	apical diverticulum
BC	—	bursa copulatrix
CKG	—	Comstock-Kellogg Gland
CT	—	constricted tube
EG	—	egg guide
PD	—	preapical diverticulum
SLPD	—	secondary lobe preapical diverticulum
TT	—	thin tube
VOV	—	ventral ovipositor valve
VST	—	vestibule

Figure 17. Bursa copulatrix and thick tube of receptaculum seminis in the Crassus and Humphreysii Groups of the genus *Barytettix*. Scale below each figure equals 0.5 mm. A-C: side views, left side of figures is dorsal. D-F: dorsal views.

A, D.   *poecilus.* México: Sinaloa, El Venadillo, T. J. Cohn, 1959 No. 214
B, E.   *humphreysii humphreysii.* Arizona: Pima Co., Sabino Canyon, M. Cazier, P. Boone, and T. J. Cohn, 1950
C, F.   *humphreysii cochisei.* Arizona: Cochise Co., Douglas, W. W. Jones, 1932
Dashed lines encompass shallow concavity in the roof of the genital chamber (see Fig. 2, p. 17, dorsal portion of the genital chamber).
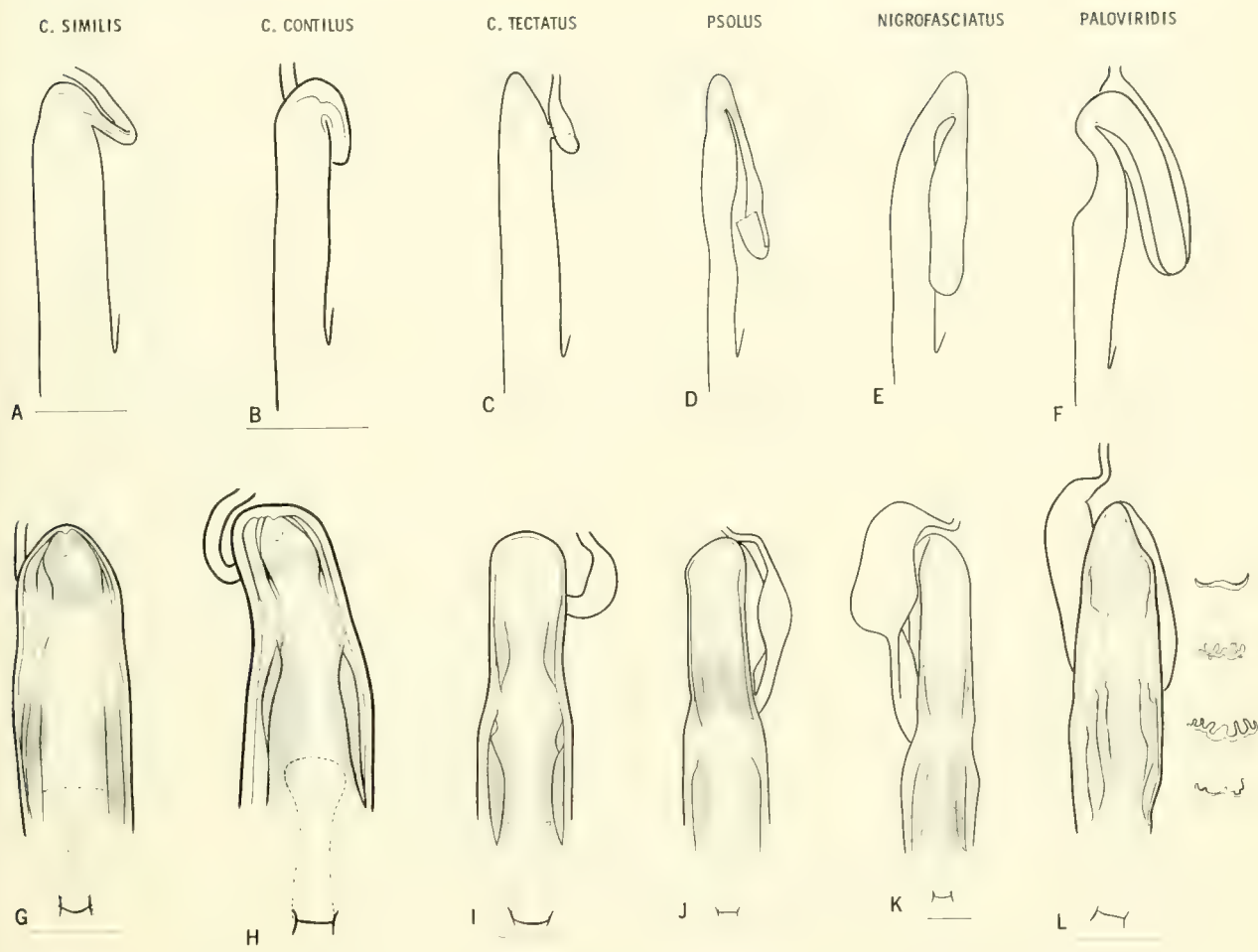
Figure 18. Bursa copulatrix and thick tube of receptaculum seminis in the Psolus Group of the genus *Barytettix*. Scale below each figure equals 1 mm. A-F: side views, left side of the figure is dorsal. G-L: dorsal views.

A, G.	*contilus similis.*	México: Sinaloa, 66 mi SE Culiacán, T. J. Cohn, 1958 No. 258
B, H.	*contilus contilus.*	México: Sinaloa, 3.1 mi NE Tepuche, T. J. Cohn, 1966 No. 39
C, I.	*contilus tectatus.*	México: Sinaloa, 7.2 mi SE Culiacán (Cerro Tule Rd.,), T. J. Cohn, 1966 No. 38
D, J.	*psolus.*	México: Sinaloa, 15.2 mi NW Culiacán, T. J. Cohn, 1966 No. 43
E, K.	*nigrofasciatus.*	México: Sinaloa, 3.6 mi NE Santa Lucía, I. J. Cantrall and T. J. Cohn, 1961 No. 50
F, L.	*paloviridis.*	México: Sinaloa, 2.5 mi NW Culiacán, I. J. Cantrall and T. J. Cohn, 1961 No. 56

Dashed lines encompass shallow concavity in the roof of the genital chamber (see Fig. 2, p. 17, dorsal portion of the genital chamber).
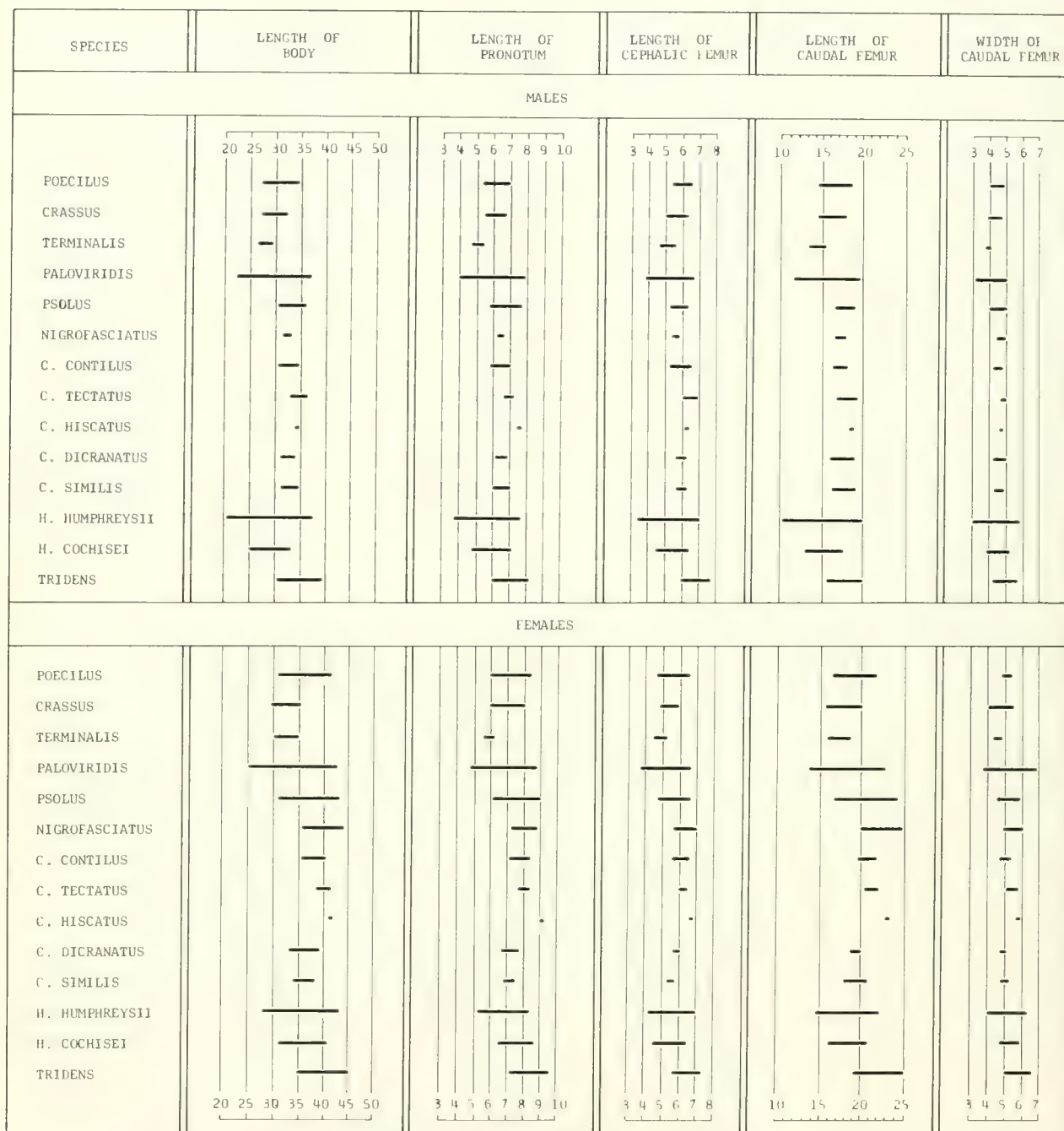
Figure 19. Summary of measurements of the species of *Barytettix*. Ranges of measurements of males (above) and females (below).
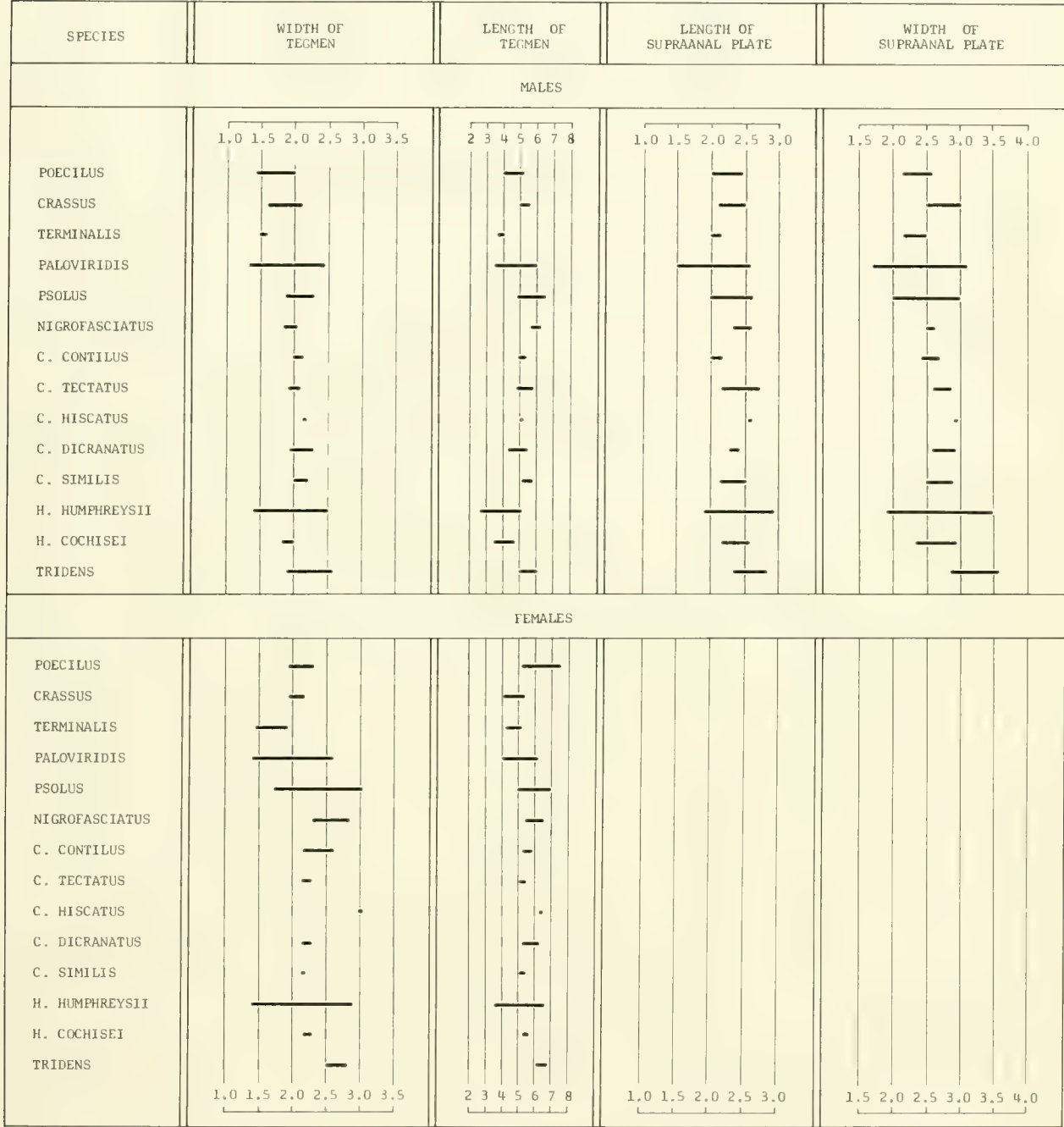
Figure 20. Summary of measurements of the species of *Barytettix*. Ranges of measurements of males (above) and females (below).